

Physiological tolerances of high temperatures in Fynbos birds: implications for climate change



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Abstract

Climate change is a reality. Numerous biological systems have already responded to changes in climate, with range shifts towards higher latitudes and altitudes being one of the most common responses to climate warming. Bioclimatic envelope modelling provides a useful method for predicting a species' future distribution under a given climate change scenario. However, these models require verification with empirical evidence, including physiological information.

Endotherm species (such as birds) have a thermal neutral zone (TNZ) which reflects the range of environmental temperatures over which minimal energy is required for thermoregulation. At temperatures above the TNZ, birds expend extra energy to facilitate evaporative water loss in order to maintain a stable body temperature, while some species increase their body temperature to conserve water. The increased costs of thermoregulation at temperatures above the TNZ can impair fitness, which could have implications for population persistence under climate change.

The Fynbos biome of South Africa is a biodiversity hotspot and is home to a rich birdlife, including six endemic bird species. Climate change models predict an increase in temperature for this biome, which may alter the ranges of many of these species, resulting in a loss of species richness and diversity. Recent MaxEnt bioclimatic envelope modelling suggests that some Fynbos bird species may be range-restricted by temperature, while others are more likely limited by other bioclimatic variables (e.g. rainfall). These data require physiological verification.

I investigated how the physiological tolerances of high temperatures vary among 12 Fynbos bird species (including the six endemic species) at a high-altitude site in the Fynbos biome. Measures of evaporative water loss (EWL), resting metabolic rate and body temperature were obtained using an open flow-through respirometry chamber at air temperatures of 24° to 42 °C. These measures were then used to determine the upper temperature limits at which energy and water expenditure, and body temperature, started to increase for each species. Limits were compared between species and used to assess whether range restriction data is supported by physiological data.

Body mass had a strong effect on physiological parameters at increasing temperatures, with larger species tending to have earlier responses at lower temperatures, but with lower rates of increase than smaller species. For example, Cape Rockjumper (*Chaetops frenatus*), with a mean body mass of 53.7 g, started to increase EWL at 31.2 °C with a rate of increase of 1.63 mg/g/h/°C, whereas Orange-breasted Sunbird (*Anthobaphes violacea*), with a mean body mass of 9.4 g, only increased EWL at 36.7 °C, but with a higher rate of increase of 5.97 mg/g/h/°C. The Cape Rockjumper exhibited the lowest heat stress threshold in terms of evaporative water loss ($T_{ewl} = 31.2$ °C) of all Fynbos species studied, as well as in comparison to similar-sized birds from other climatic regions of the world (e.g. $T_{ewl} = 40.2$ °C for desert-dwelling White-browed Sparrow-weaver (*Plocepasser mahali*) and $T_{ewl} = 34.3$ °C for tropical Monk Parakeet (*Myiopsitta monachus*)). This could support MaxEnt predictions about range restriction in the Cape Rockjumper and requires special attention in light of future climate warming in the region.

My findings suggest that some Fynbos species show relatively low heat tolerance compared to birds from hotter environments. The relative vulnerabilities of different Fynbos bird species to climate warming could provide insight into changes in the structure and therefore ecological functioning of the Fynbos avian community in the near future.

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Plagiarism declaration

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own.
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Robyn Milne

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1. Introduction

Climate and climate change

Abiotic and biotic features of the environment are fundamental in determining the abundance and distribution of wildlife across the planet (Andrewartha & Birch 1954; MacArthur 1958). Climate-related abiotic factors (e.g. temperature and precipitation) are particularly important, as they directly influence an organism's survival (Thacker et al. 1997), growth (Went 1949; Vinagre et al. 2012) and reproduction (Hutchins 1947; Spotila 1972). There is a long history of research into the effects of climate on biodiversity (reviewed by Parmesan 2006). Nearly a century ago, Grinnell (1917) described how temperature limits the geographic ranges of species. This set the groundwork for many further studies linking species' ranges to climate (e.g. Andrewartha & Birch 1954; MacArthur 1958) and, more recently, to climatic changes (e.g. Thomas & Lennon 1999; Lenoir et al. 2008; Frei et al. 2014). Considering the importance of climate for biodiversity, the realization that "the planet is now committed to anthropogenic climate change..." (Chown et al. 2010), is greatly concerning from a conservation perspective.

Climate change: today and tomorrow

Human-altered landscapes dominate the planet (Ellis & Ramankutty 2008), but even the remaining "natural" landscapes have felt the weight of the human footprint in the form of climate change (Chown 2010). In fact, climate change has been described as the largest imminent threat to biodiversity as its effects are experienced in almost every biome (Thomas et al. 2004; Millennium Ecosystem Assessment 2005). Additionally, the effects of climate change exacerbate the effects of other anthropogenic threats, such as habitat destruction, pollution and species introductions (Root et al. 2003; Travis 2003).

There is no longer doubt that concentrations of greenhouse gases have been rising since the mid 18th century due to fossil fuel combustion, and that this is altering global and regional climates (IPCC 2013). Climate change is predicted to alter life history strategies of individual organisms (Musolin et

al. 2010), temporal and spatial patterns of population abundance (Rutherford et al. 1999; Kearney et al. 2009; Huntley et al. 2011) and species richness (Huntley & Barnard 2012), and ultimately increase the risk of extinction (Thomas et al. 2004). Thomas et al. (2004) predicted that 34 to 58% of species they investigated will become extinct by 2050, depending on the climate change scenario (Thomas et al. 2004). This is significantly higher than the predicted extinction risk from habitat loss, which is between 1 and 29%, depending on the biome (Thomas et al. 2004).

However, climate change is not just a looming threat on the horizon; it is presently an undeniable reality (Easterling et al. 1997; Karl & Knight 1998; Hughes 2000; Root et al. 2003; reviewed in Parmesan 2006). A recent report by the Intergovernmental Panel on Climate Change (IPCC) revealed that mean temperatures are rising and glaciers are melting, carbon dioxide levels are the highest they have been in 800 000 years and the Earth's surface is currently warmer than it has been since the start of direct monitoring in 1850 (IPCC 2013).

Numerous biological systems have already responded to changes in climatic patterns. There have been direct effects on the physiology of both plants (Keeling et al. 1996; Myneni et al. 1997) and animals (Pörtner & Knust 2007), the timing of migration and breeding is changing (Brown et al. 1999; Møller et al. 2006; Post et al. 2008) and species' distributions are shifting (Smith 1994; Parmesan et al. 1999; Thomas & Lennon 1999; Lenoir et al. 2008; Chen et al. 2011). These effects have altered community structure and composition (Holbrook et al. 1997; Genner et al. 2004; Le Roux & McGeoch 2008) and caused population declines (Both et al. 2006; Foden et al. 2007; Williams & Middleton 2008). In addition, several climate change-related extinctions have been documented at both the population level (e.g. in pikas (*Ochotona prince*), Beever et al. 2003; and Arctic polar bears (*Ursus maritimus*), Derocher 2005) and the species level (e.g. in harlequin frogs (*Atelopus* spp.), Pounds et al. 2006).

Climate change manifests itself in various forms, but changes in air temperature are likely to have some of the most detrimental impacts on biodiversity (IPCC 2007b). This is disconcerting given that the Earth is predicted to become warmer in the next few decades than it has been in the past 40

million years (IPCC 2007a). Not only are organisms experiencing the direct lethal effects of prolonged exposure to high temperatures (Dawson 1954; Hazel 1995; Daniel et al. 2009), they are also suffering from numerous sub-lethal fitness effects. For example, at high temperatures lizards (*Sceloporus* spp.) in Mexican deserts avoid direct sunlight by moving into shaded rock crevices, but due to rising temperatures they no longer have enough time per day to forage for energy to reproduce; hence many populations have gone extinct (Sinervo et al. 2010).

Shifting geographical distributions is one of the most common responses to climate warming (reviewed in Parmesan 2006). Various species have already shifted their ranges towards higher latitudes and elevations in search of cooler temperatures (Smith 1994; Parmesan et al. 1999; Thomas & Lennon 1999; Parmesan & Yohe 2003; Hickling et al. 2006). For example, warming has most likely compelled bird species from lower altitudes to colonise higher regions in the montane cloud forest of Costa Rica (Pounds et al. 1999). However, such range shifts can only take place if suitable new sites remain available (Chown et al. 2010). For many species, this will not be the case given the current rate of habitat transformation and degradation (Travis 2003).

Assessing species vulnerability to climate change

The magnitude and direction of climate-driven range shifts will depend on the life history strategies and habitat requirements of the species involved, as well as characteristics of the landscape it occupies (Hill et al. 1999; Okes et al. 2008). Certain species may thus be more susceptible than others to the negative consequences of climate change (Crick 2004; Brommer & Møller 2010). Highly vulnerable species are likely to be those with already-restricted geographical ranges (such as high altitudinal or polar ranges), ranges within centres of endemism or ranges that have already contracted as a consequence of anthropogenic-associated habitat loss (Thuiller et al. 2005; Huntley & Barnard 2012). Furthermore, highly specialised species (Thuiller et al. 2005) and slow dispersers are also more likely to be vulnerable (Broennimann et al. 2006).

Bioclimatic envelope models, mechanistic models, and their limitations

Most current approaches to predicting climate-mediated range changes use correlative methods, such as bioclimatic envelope modelling (e.g. Peterson 2001; Berry et al. 2002; Pearson et al. 2002; Simmons et al. 2004; Coetzee et al. 2009). These models create a 'climate envelope' which relates a population's present distribution to a range of climatic variables under which it currently exists (Pearson & Dawson 2003). The population's future range is then modelled under climate change projections, assuming the present-day envelope is retained (Bakkenes et al. 2002; Peterson et al. 2002; Pearson & Dawson 2003). An early example of such a modelling strategy is the work of Johnston (1924) who successfully predicted the spread of an invasive cactus in Australia, based on climatic features of its native North American range. In the seminal work by Huntley et al. (1995), range retractions for eight European plant species under future warming scenarios were predicted by fitting various climate response surfaces relating to three bioclimatic variables. Now, nearly two decades later, predictions such as these are materialising as seen in, for example, the recent report of range contractions in alpine montane birds (Lehikoinen et al. 2014).

However, some of the assumptions inherent in bioclimatic envelope models are questionable (Pearson & Dawson 2003; Kearney & Porter 2009; McKechnie et al. 2012); e.g. that climate alone limits the survival of the population (McKechnie et al. 2012), that the present distribution of the population is in equilibrium with the current climate (Pearson & Dawson 2003; Boyles et al. 2011) and that the population will shift its range in response to climatic changes (Boyles et al. 2011). For example, work by Glanville et al. (2012) and Smit et al. (2013) suggests that a species's present-day distribution does not necessarily represent its climatic tolerance, but rather a compromise between biotic and abiotic interactions.

Bioclimatic envelope models are thus purely correlative and provide little insight into the physiological and behavioural mechanisms that influence an organism's fitness and performance within its environment (Williams et al. 2008; Huntley et al. 2010). Predictions made by these models need to be supported by empirical information on the species's intrinsic biology. Mechanistic models are one alternative to bioclimatic envelope modelling. These models incorporate data on

morphological, physiological and behavioural traits of the species, over and above detailed environmental and spatial data (Kearney & Porter 2009). Mechanistic models are thus likely to be more robust than bioclimatic models, but their inherent complexity can make them difficult to parameterise (Pearson & Dawson 2003).

Bioclimatic envelope modelling therefore remains a useful and practical technique for predicting climate-related range changes, provided the outcomes can be verified empirically (Pearson & Dawson 2003; Kearney & Porter 2009). It has been suggested that change in environmental temperature is the most predictable aspect of climate change (IPCC 2007a). Characterising species' physiological tolerances for increasing temperatures is thus one of the most effective ways of verifying bioclimatic model suggestions that some species might be temperature limited (Helmuth et al. 2005; Kearney & Porter 2009).

How endotherms handle the heat

Thermoregulation in endotherms

The evolution of endothermy enabled animals such as mammals and birds to inhabit ecological niches generally inhospitable to ectotherms, (e.g. at high latitudes and altitudes, McNab 2012). Endotherms are able to regulate a high and stable body temperature (T_b , generally 39°-43 °C in birds and 37°-38 °C in mammals), despite fluctuating environmental temperatures, by endogenous adjustments in heat production and heat loss (Pörtner 2004; Angilletta et al. 2010). This is energy-demanding and reduces energy available for growth and reproduction (Pörtner 2004; Angilletta Jr. 2009). However, it also confers certain metabolic advantages. For example, many biochemical reactions occur at a faster rate at higher temperatures (Hochachka & Somero 2002) and having a smaller range of possible T_b s means that each body cell only needs to generate enough macromolecules to function within this range (Heinrich 1977).

The physiological response of endotherms to temperature is generally non-linear (Scholander et al. 1950; Calder & King 1974). Endothermic species have a thermal neutral zone (TNZ), which reflects

the range of environmental temperatures over which the animal produces minimal metabolic heat and no additional energy expenditure is required for thermoregulation (Scholander et al. 1950; Calder & King 1974).

As the environmental temperature falls below the TNZ, metabolism is increased and extra energy is expended to generate heat and maintain optimal T_b (Withers 1992). At environmental temperatures above the TNZ, endotherms can employ one of two physiological strategies for thermoregulation. First, some species are able to use facultative hyperthermia (or heat storage). This involves increasing T_b above normal levels in order to maintain a temperature gradient between body and air temperatures, which allows passive heat loss and reduces the need for evaporative cooling (Calder & King 1974; Weathers & Schoenbaechler 1976). Alternatively, many endotherms maintain a constant T_b by facilitating evaporative heat loss at temperatures exceeding the TNZ, although this comes at a cost in terms of water and energy (Calder & King 1974; Angilletta et al. 2010).

Evaporative water loss (EWL) involves the evaporation of water from respiratory passages or the outermost surface of the skin, fur or feathers (reviewed by Tieleman & Williams 1999; Cain et al. 2006). EWL can be an extremely efficient means of heat dissipation. For example, the Common Poorwill (*Phalaenoptilus nuttallii*) dissipates by evaporation an amount of heat that is more than 160% of its metabolic heat production at an ambient temperature of 40 °C (Bartholomew et al. 1962). However, EWL is energetically costly. Prolonged reliance on EWL can lead to substantial losses in body mass (Maloney et al. 1999) and a significant increase in the risk of dehydration (Studier et al. 1970) as well as hypocapnia and alkalosis due to the excessive removal of carbon dioxide from the blood (Phillips et al. 1985). This impairs further thermoregulation and overall performance and may even lead to death (Tieleman et al. 2002; Angilletta et al. 2010).

In order to avoid some of the physiological costs of heat dissipation, endotherms also use behavioural strategies to keep cool. For example, endotherms select cooler microsites to reduce environmental heat load (Willoughby 1971; Austin 1976; Wolf 2000) or shift towards a more inactive state to reduce metabolic heat load (Austin 1976; Ricklefs & Hainsworth 1968).

Failure to avoid excessive heat loads and/or dissipate heat efficiently can be fatal (Dawson 1954), since extreme high temperatures alter the microenvironment in body cells (Hazel 1995; Daniel et al. 2009), impairing the reproduction and survival of the organism (Dawson 1954; Hochachko & Somero 2002).

Avian thermoregulation

Birds are extraordinary endotherms in that their lungs are twice as efficient at gaseous exchange as the mammalian lung, which helps fuel their higher metabolic rates (Pörtner 2004; McNab 2012). Therefore, birds are less limited by oxygen at high temperatures, which supports their active lifestyles (Pörtner 2004) and the high energy requirements of flight (Phillips et al. 1985).

Birds get rid of excess heat by passively increasing blood flow to the beak (Tattersall et al. 2009) or the skin of the feet and legs (Phillips et al. 1985), or by spreading their wings to expose the thin undersides of the wings (Phillips et al. 1985). Alternatively, some birds employ gular fluttering (Bartholomew et al. 1962) or panting (Lasiewski & Bartholomew 1966) to increase evaporation of water and heat from nasal and tracheal passages. Others additionally use adaptive hyperthermia (Calder & King 1974). For example, at air temperatures of 38 °C, the Pyrrhuloxia (*Cardinalis sinuatus*) from North America decreases evaporative water loss by half as a result of a 2.3 °C increase in T_b (Weathers 1981).

Behaviourally, birds are most active during the morning and evening when it is coolest (Ricklefs & Hainsworth 1968), and often seek shaded microsites to avoid direct sun (Willoughby 1971; Austin 1976; Wolf 2000). In addition, they select energy- and protein-rich foods to reduce foraging time and metabolic heat loads (Phillips et al. 1985; Wolf 2000).

The impact of climate change on endotherms

As climate warming increases the frequency of days with high environmental temperatures, endotherms will have no choice but to channel limited resources and energy to thermoregulation, leaving less for other important processes such as foraging, growth and reproduction (Boyles et al.

2011; du Plessis et al. 2012; Cunningham et al. 2013). This could have implications for population persistence under climate change (Sinervo et al. 2010). It remains to be seen whether endotherms will be able to shift ranges quickly enough to avoid changes in environmental temperatures above the TNZ (Boyles et al. 2011) and there is also the possibility that rapid evolutionary change will alter the tolerance ranges of animals as the climate warms in future (Pearson & Dawson 2003).

Avian responses to climate change

Because of their highly mobile lifestyles, birds should be able to respond to climate change quicker than more sedentary organisms such as plants or terrestrial mammals (Simmons et al. 2004). Indeed, according to Crick (2004), the field of ornithology offers some of the best examples of the consequences of recent climate change on global biodiversity. In addition, birds are relatively easy to recognise, observe and study, and their distributions are amongst the most well-known of all animals (Møller et al. 2010). Furthermore, birds may be especially sensitive to changes in environmental temperature due to their generally diurnal habits, relatively small body sizes, and high T_b s and metabolic rates compared to their mammalian counterparts (Pörtner 2004; McKechnie & Wolf 2010). Unsurprisingly then, birds have been identified as particularly good indicators of climatic changes (Crick 2004).

The effects of climate change are already being felt in various bird species (Crick 2004). These include changes in migration timing (Hüppop & Hüppop 2003), breeding biology (Thompson & Ollason 2001) and population sizes (Cunningham & Moors 1994), as well as numerous non-lethal fitness effects as a consequence of having to balance foraging and heat dissipation under prolonged exposure to high temperatures (McKechnie & Wolf 2010; du Plessis et al. 2012; Cunningham et al. 2013). Birds are also shifting their ranges in search of more climatically suitable habitats (Pounds et al. 1999; Lehikoinen et al. 2014).

Different bird species under the same thermal conditions should differ in their physiological responses to high temperatures, due to variation in morphological, physiological and ecological traits (Weathers 1981; Huey 1991). Body size is one such trait that is important in explaining these varied responses

(Weathers 1981). The rate of heat exchange between an animal and its environment is proportional to the organism's surface area-to-volume ratio (Schmidt-Nielsen 1984; Calder 1996). In general, smaller birds have higher surface area-to-volume ratios (Austin 1976) and can thus gain and lose heat passively via conduction, convection and radiation faster than larger birds. This also means that smaller birds have higher mass-specific rates of EWL compared to larger birds (Stevenson & Bryant 2000), which show a more gradual response to increasing temperatures (Austin 1976; McKechnie & Wolf 2010). Therefore, while smaller species lose water faster and have a higher risk of dehydration, larger species struggle to get rid of excess heat, placing them at risk of heat stress (Weathers 1981; Tieleman & Williams 1999) and subsequent hyperthermia (McKechnie & Wolf 2010). Behaviourally, smaller species may be able to utilise cooler microsites more easily than larger birds, which may provide temporary relief from intense heat (Wolf & Walsberg 1996b). However, retreating to thermal refugia reduces time available for foraging and has been shown to have unfavourable consequences for body condition, fitness and survival (Walsberg 1993; Sinervo et al. 2010).

The nutritional properties of different food types also affect energy expenditure, thereby partially dictating an animal's selection of food items and influencing its physiological response to environmental change (Tieleman & Williams 2002b). Granivorous birds acquire little water from their food and are thus likely to pay greater EWL costs at high temperatures when water resources are limited (Bartholomew & Cade 1963). Insectivorous species on the other hand satisfy most of their water needs via their diets (Bartholomew & Cade 1963; Bicudo et al. 2010). In addition, birds with highly specialised dietary niches may be more vulnerable to climatic changes if their food sources become temporally or spatially decoupled from them (Both & Visser 2001).

The Fynbos biome

Small, superb, susceptible

Africa has been identified as the most vulnerable continent to the impacts of anthropogenic climate change (Hulme 1996; IPCC 2001) and is predicted to become warmer and drier in the future (IPCC 2001). The Fynbos biome is situated in the south-western corner of the African continent

(Conservation International 2014). It has a Mediterranean climate (Klausmeyer & Shaw 2009) and comprises numerous mountain ranges reaching altitudes of over 1 500 m above sea level (BirdLife International 2014). The biome is a global biodiversity hotspot (Myers et al. 2000) and is the smallest, but one of the most species-rich of the world's six floral kingdoms (Cowling et al. 1998; Conservation International 2014), boasting more than 8 500 vascular plant species of which nearly 70% are endemic to the biome (Cowling & Hilton-Taylor 1994). The region is also home to a rich birdlife, including six endemic passerine bird species (BirdLife International 2014), many of which are important for maintaining vital ecosystem functions, such as pollination (e.g. Cape Sugarbird (*Promerops cafer*) and Orange-breasted Sunbird (*Anthobaphes violacea*), Huntley & Barnard 2012).

By 2100, the Mediterranean biomes of the world are projected to suffer the greatest proportional loss of biodiversity of all terrestrial biomes owing to a multitude of threats (Sala et al. 2000). The Fynbos biome's mild climate and close proximity to the ocean make it particularly susceptible to anthropogenic transformation (Sala et al. 2000; Hoekstra et al. 2005), with the greatest visible human footprint in low-lying areas of the biome (Rebelo 1992). More than 30% of the region has already undergone major transformation into agricultural land (Huntley & Barnard 2012), while the remaining area has largely succumbed to alien plant invasions (Richardson et al. 1996), infrastructure development (Rebelo 1992) and/or poor management (Huntley & Barnard 2012). Large-scale habitat transformation of the Fynbos region has fragmented numerous animal and plant populations, reducing population fitness and species richness (Bond et al. 1988; Rebelo 1992). Unsurprisingly then, some of the biome's more than 100 different habitat types, such as the Renosterveld vegetation type, are already considered endangered (Cowling et al. 1986). However, while montane habitats appear to be relatively well-protected when it comes to human-induced land use change (Kemper et al. 1999), it is here that climate change is predicted to hit hardest (Huntley et al. 2007; Gonzalez et al. 2010).

Climate change and the Fynbos avian community

Over the past few decades, large areas of the Fynbos biome have experienced increasing temperatures and reduced rainfall (Tyson et al. 2002; Midgley et al. 2003; Hockey & Midgley 2009). Continuation of these trends is predicted to reduce the ranges of various bird species, resulting in a loss of avian

species richness and diversity, with numerous knock-on effects for the ecosystem at a broader scale (Huntley & Barnard 2012).

The impacts of climate change on biodiversity are less well documented in montane regions compared to low-lying areas (Parmesan 2006). Despite this, montane ecosystems may be particularly vulnerable to temperature increases (Frei et al. 2014), with 20th century warming in montane regions, such as the European Alps, occurring nearly three times faster than the global average increase in air temperature (IPCC 2007b; Appenzeller et al. 2008). In addition, the available literature shows a general uphill shifting trend in, for example, alpine plants (Grabherr et al. 1996), dung beetles (Menendez et al. 2013), butterflies (Wilson et al. 2005) and birds (Pounds et al. 1999; Lehikoinen et al. 2014) as a consequence of climate change-mediated temperature increases.

According to Southern African Bird Atlas Project (SABAP) data, Fynbos endemic bird species are faring less well in terms of reported range and reporting rates than a suite of ecologically and morphologically similar species (Lee & Barnard 2012). Recent range mapping and bioclimatic modelling suggests that some Fynbos bird species, occurring mostly at the highest altitudes, may be range-restricted by maximum temperatures (e.g. Cape Rockjumper (*Chaetops frenatus*) and Protea Seedeater (*Serinus leucopterus*)), whereas others are more likely restricted by different bioclimatic variables (e.g. rainfall and seasonality which are linked to the Mediterranean climate; A.T.K. Lee and P. Barnard, unpublished data). Additionally, the Cape Rockjumper was ranked as one of the most susceptible birds to climate change in southern Africa, due to its preference for mountain slopes and peaks and its restriction to the southern Fynbos biome (Simmons et al. 2004). Despite this, all six species endemic to the Fynbos biome are listed as Least Concern on the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List (IUCN 2013) and data are sorely lacking on the temperature tolerances of birds in this biome.

Rationale for my study

The responses of organisms to climate warming are likely to influence both the conservation and policy arenas, as well as pest and disease management (Kearney et al. 2009). Our ability to take swift action in response to climatic changes will require a thorough knowledge of how these changes affect biodiversity. It is imperative that the vulnerabilities of different species to climate change be determined in order to implement tailor-made adaptation and/or mitigation strategies (Huey et al. 2012; Sax et al. 2013). There is scant information on the vulnerability of Southern Hemisphere organisms to climate change (Root et al. 2003) and particularly in Africa (Simmons et al. 2004). This study aims to address this shortfall at the southern tip of the African continent.

Characterising the physiological temperature tolerances of birds in the Fynbos biome will allow us to assess whether recent bioclimatic model data suggesting that some endemic species are temperature-limited (A.T.K. Lee & P. Barnard, unpublished data), are supported by physiological data. This will provide a valuable indication of the relative vulnerabilities of different species to climate change, as well as an assessment of the likely predictive power of the bioclimatic envelope models.

I measured the physiological temperature tolerances of 12 passerine bird species in the Fynbos biome of south-western South Africa. These include the six species endemic to the Fynbos biome as well as six species with broader distributions falling within at least one other biome, in order to investigate how Fynbos endemic species compare (in terms of thermal responses) with birds that have a more generalised distribution. The study also provided a useful opportunity to assess whether temperature tolerances differ between species with different mean body sizes and between species occupying different dietary niches.

Results from this study will help us understand the implications of climate warming for Fynbos bird species. This will provide insight into the possible alterations in the structure and ecological functioning of the Fynbos avian community in the near future (Huey et al. 2012). Additionally, this data will provide vital novel information about the thermal physiology of Fynbos bird species, a subject which, to date, remains wholly unexplored.

This study aims to answer the following key questions, by implementing the objectives listed below each:

Question 1: How do the physiological tolerances of high temperatures vary among Fynbos bird species?

- Document the upper bound of the TNZ in 12 Fynbos bird species.
- Investigate EWL responses at a range of ambient temperatures within and above the TNZ.
- Determine how body temperatures change in response to increasing ambient temperatures.
- Assess temperatures associated with the onset of panting behaviour in the 12 species.

Question 2: Do physiological temperature tolerances differ between:

(a) species predicted to be temperature-limited and those predicted to be limited by other bioclimatic factors;

- Compare physiological information with the latest information on the factors limiting range distribution in each species.

(b) species with different average body sizes, occupying different dietary niches, or Fynbos endemics versus those not restricted to this biome?

- Assess whether there are consistent differences in physiological temperature tolerances between species with different average body sizes, species from different dietary guilds, and between endemic and non-endemic species.

Question 3: How do physiological tolerances of Fynbos birds compare to those in other biomes?

- Assess whether there are differences in evaporative water loss responses of the 12 Fynbos bird species from this study and 33 other species occupying a variety of biomes globally.

Question 4: What are the implications for different species under climate change?

- Discuss the potential vulnerabilities (in terms of tolerances for high temperatures) of different bird species to climate warming in the Fynbos biome in future.
- Identify shortcomings from this and similar studies.
- Suggest future avenues of research to improve the quality of conservation efforts.

2. Methods

Ethics statement

The methods used in this study were approved by the University of Cape Town Science Faculty Animal Ethics Committee (clearance # 2013/V23/PR). The study was carried out on private land (Blue Hill Nature Reserve) with permission of the landowners and Cape Nature, South Africa (permit # AAA041-00043-0056).

Study site

The study was conducted from 23 September to 29 November, 2013, at Blue Hill Nature Reserve (BHNR; 33.59S; 23.41E; 1 000 - 1 530 m above sea level), a 2 230 ha reserve situated on the western border of the Baviaanskloof Wilderness Area, Western Cape, South Africa (Figure 1). The area falls within the Fynbos biome, which is restricted to the southwestern corner of South Africa (Mucina & Rutherford 2006). This biome comprises Fynbos, Renosterveld and Strandveld vegetation elements, and is generally characterised by small-leaved, evergreen shrubs that require fire for regeneration (Mucina & Rutherford 2006).

BHNR has a mountainous topography and the vegetation consists mainly of Mountain Fynbos (Figure 1B), which typically is dominated by the Proteaceae, Ericaceae and/or Restionaceae (Mucina & Rutherford 2006; Lee & Barnard 2013). South-facing slopes are dominated by mature stands of *Protea* spp. and *Erica* spp. on slopes that have not burnt for >10 years, or *Restio* spp. and *Erica* spp. in more recently burnt areas. North- and east-facing slopes are dominated by Sandolienveld, consisting of a mix of *Elytropappus* spp. (Renosterbos), *Dodonea viscosa* (Sandolien) and some Fynbos elements (Vlok et al. 2005). Fynbos riverine thicket occurs along the three small streams and secondary Renosterveld dominates areas of land previously cleared for agriculture (Lee & Barnard 2013). Refer to Figure 1B for a map of the major vegetation types at BHNR.

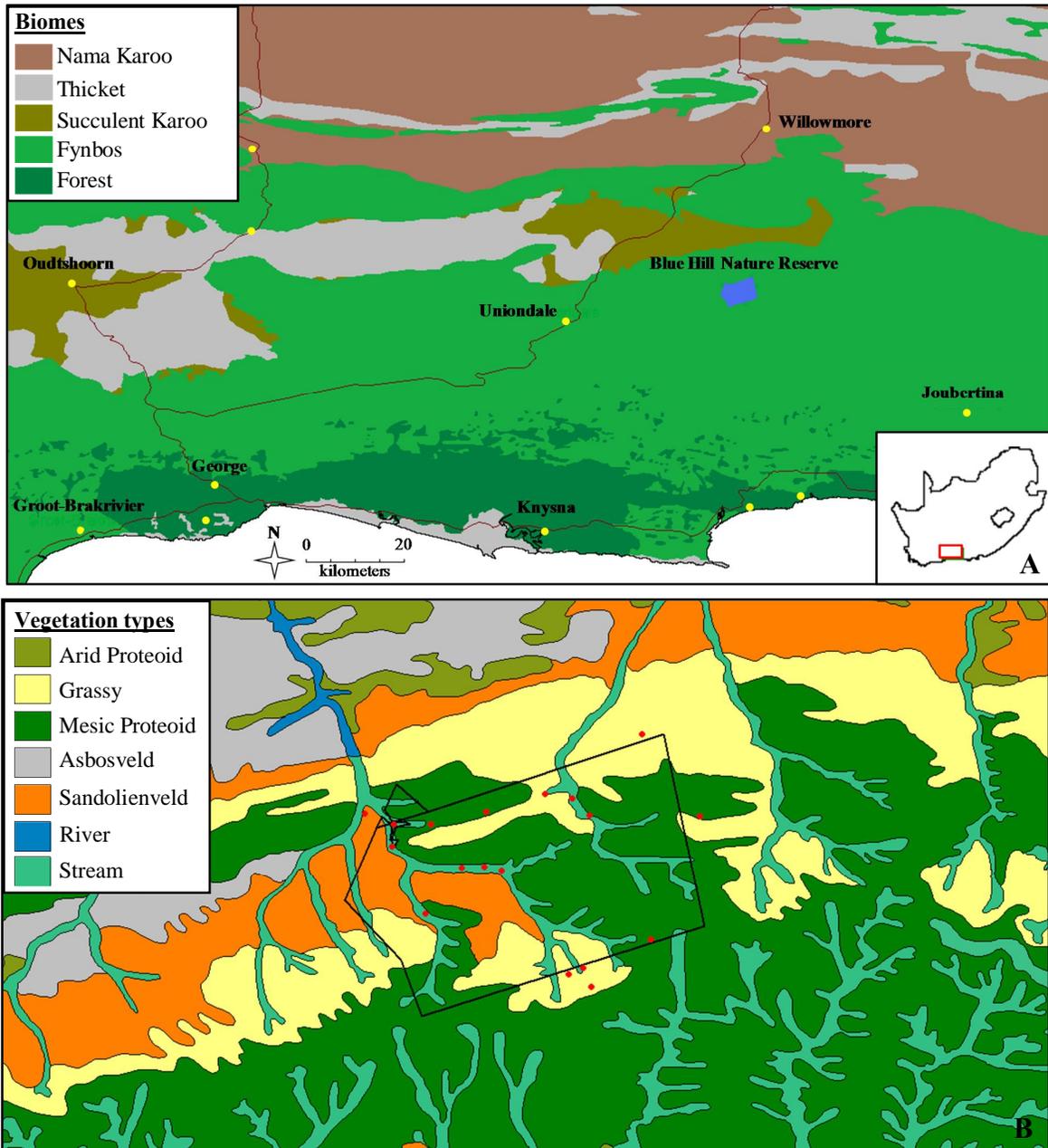


Figure 1. **A.** Map showing the location of Blue Hill Nature Reserve (blue) within the Fynbos biome, Western Cape, South Africa. Figure also indicates the surrounding biomes (see legend) and nearby settlements (yellow dots). Closest town: Uniondale (40 km away). **B.** Map of Blue Hill Nature Reserve showing the property boundary (black line) and the locations of capture sites (red dots) scattered amongst the different vegetation types (see legend).

The area is characterised by mild to warm summers and cold winters, with snow occurring on the mountains during peak winter season (Mucina & Rutherford 2006). The study period coincided with spring and early summer in the region. Mean daily (24 h period) temperatures during this period

ranged from 6.6° to 24.5 °C, as recorded by an onsite weather station (Davis Vantage Vue, USA). The study site falls within an aseasonal rainfall region, as it lies in a transition zone between the summer and winter rainfall regions of South Africa. Mean annual rainfall for the area is 397 ± 98 mm (Lee & Barnard 2013).

Study species and capture methods

Data on the physiological temperature tolerances of 12 different passerine bird species were collected. These included the six species endemic to the Fynbos biome and six species that occur regularly within Fynbos, but are not restricted to this biome (Table 1). Non-endemic species were selected to provide as close as possible a match to an endemic counterpart (such that six õpairsö were studied), in terms of both body size and dietary guild. In addition, non-endemic species that were relatively abundant at the study site were favoured in order to ensure capture success. All study species are currently listed as Least Concern according to the IUCN Redlist (IUCN 2013). Information on dietary guild and degree of endemism to the Fynbos biome for each species was obtained from Hockey et al. (2005).

Table 1. A summary of the 12 bird species selected for this study. The table shows scientific names of species pairs, statuses regarding endemism to the Fynbos biome (F = Fynbos endemic, N = non-endemic), dietary guilds, sample sizes (n) and mean body masses at time of capture (Mean $M_b \pm$ Std. Error, g).

Pair	Species	Scientific name	Endemism	Dietary guild	n	Mean $M_b \pm$ Std. Error (g)
1	Cape Sugarbird	<i>Promerops cafer</i>	F	Nectarivore	11	35.6 ± 1.2
1	Malachite Sunbird	<i>Nectarinia famosa</i>	N	Nectarivore	5	15.1 ± 0.9
2	Orange-breasted Sunbird	<i>Anthobaphes violacea</i>	F	Nectarivore	10	9.4 ± 0.4
2	Southern Double-collared Sunbird	<i>Cinnyris chalybeus</i>	N	Nectarivore	10	7.6 ± 0.2
3	Cape Siskin	<i>Crithagra totta</i>	F	Granivore	10	12.7 ± 0.3
3	Cape Canary	<i>Serinus canicollis</i>	N	Granivore	4	15.0 ± 0.4
4	Protea Seedeater	<i>Crithagra leucoptera</i>	F	Granivore	9	20.5 ± 0.4
4	Cape Bunting	<i>Emberiza capensis</i>	N	Granivore	10	20.0 ± 0.5
5	Victorinõ Warbler	<i>Cryptillas victorini</i>	F	Insectivore	6	16.6 ± 0.4
5	Cape Grassbird	<i>Sphenoecus afer</i>	N	Insectivore	5	30.0 ± 1.1
6	Cape Rockjumper	<i>Chaetops frenatus</i>	F	Insectivore	10	53.7 ± 1.4
6	Familiar Chat	<i>Cercomela familiaris</i>	N	Insectivore	10	20.5 ± 0.4

All birds were captured during the active phase of their circadian cycle using mist-nets and/or spring-traps baited with mealworms. Capturing took place every day from dawn to midday. After capture, each bird was weighed (accurate to 0.1 g) and ringed with an aluminium band for identification according to South African Bird Ringing Unit (SAFRING) guidelines (De Beer et al. 2001). Age, sex (if sexually dimorphic) and moult status were determined from plumage examination and only adult individuals were used in the study (juveniles were released immediately after ringing). All individuals showing clear signs of breeding activity, such as an abdominal brood patch or smear marks around the beak from provisioning young, also were released in order to minimise disruption of reproductive behaviour. The remaining birds were transported in cloth bags to a field laboratory on the reserve to initiate physiological measurements.

Data collected

Metabolic measurements

Measurements of evaporative water loss (EWL, measured as water vapour production (VH_2O)) and resting metabolic rate (measured as carbon dioxide production (VCO_2) and oxygen consumption (VO_2)) were obtained at air temperatures (T_a) ranging from 24° to 42 °C using an open-flow-through field respirometry system (Figure 2). Birds were placed individually in respirometry chambers constructed from airtight plastic containers (1.9, 4 or 6 L, depending on the size of the bird). A 0.5 cm layer of mineral oil was placed in the bottom of each chamber to prevent evaporation from urine and faeces, thus excluding these as sources of water in measurements. Birds were placed on a wire mesh platform positioned 5 to 10 cm above the oil layer, with large enough holes to allow faeces to fall through. The respirometry chamber containing a bird was placed within an insulated environmental chamber constructed by lining the interior of a 100 L cooler box with copper tubing (Smit & McKechnie 2010). The temperature within the respirometry chamber was regulated by pumping temperature-controlled water from a circulating water bath (FRB22D, Lasec, Cape Town, South Africa) through the copper tubing in the environmental chamber using a small water pump. An electric fan was used to ensure air circulation within the cooler box. Air temperature within the

respirometry chamber was measured using a thermistor probe (model TC100, Sable Systems, Las Vegas, NV, USA) inserted into the chamber through a small hole in the lid.

Atmospheric air from outside the building was pushed through the system using a GAST air compressor (MOA-P101-CD, GAST Manufacturing, Inc., Michigan, USA). Water vapour was scrubbed from the air using a silica gel and a drierite column connected in series. The flow rate into the respirometry chamber was regulated using an FMA-series mass flow controller (Omega, Bridgeport, NJ, USA) calibrated using a flow-bubble meter. Flow rates of between 1.0 and 5.5 L/min were used throughout measurements, depending on the species and T_a . These flow rates were selected to ensure low water vapour pressures in the chamber, thus ensuring high vapour pressure deficits (> 5 kPa) to maximise the efficiency of evaporative cooling. Maintaining low humidity in the chamber appeared to significantly reduce the likelihood of stress in the birds at higher air temperatures. Excurrent air from the respirometry chamber and a reference air supply (baseline air sampled downstream of scrubbers) was sub-sampled using an SS1 sub-sampler (Sable Systems), and a TR-RM8 Respirometry Multiplexer (V3, Sable Systems). Baseline water vapour pressure (kPa) and CO_2 and O_2 concentrations (%) were obtained from the reference air channel for at least 10 min before

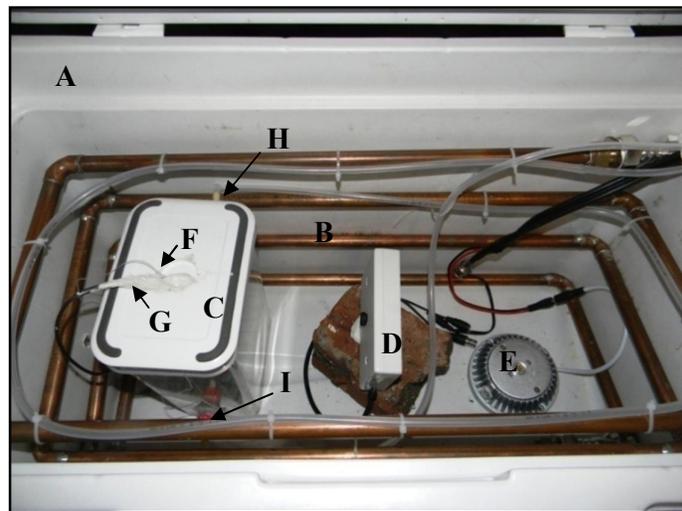


Figure 2. Open-flow-through field respirometry system showing A) environmental chamber, B) copper coil for regulating T_a , C) plastic respirometry chamber, D) video camera, E) infrared light source, F) thermocouple (inserted into the cloaca of the bird inside the chamber), G) thermistor probe for measuring T_a inside the chamber, H) incurrent air inlet, and I) excurrent air outlet.

placing the bird into the respirometry chamber, as well as for 5 min following every experimental temperature period during the trial by manually switching between airstreams. Sub-sampled air first passed through a water analyser (RH-300, Sable Systems) to measure water vapour pressure. Air was then pulled through a silica gel column to remove water vapour before passing through a CO₂ analyser (Ca-10a, Sable Systems) to measure the CO₂ concentration. At the beginning of the study both the CO₂ and water analysers were zeroed using pure nitrogen. The CO₂ analyser was calibrated against an analytically certified gas with a known CO₂ concentration of 1 500 ppm. The water analyser was calibrated by calculating the water vapour pressure of air saturated at 16°C. The air sample then passed through a soda lime/silica gel column to remove CO₂ and water vapour, respectively, before entering an O₂ analyser (Fc-10a, Sable Systems) to measure the fractional O₂ concentration. The O₂ analyser was calibrated to a fractional O₂ concentration of 20.95% at the start of each experimental trial. Outputs from these three gas analysers were digitised using a Universal Interface II system (Sable Systems) and recorded with a sampling interval of 1 second using Expedata data acquisition software (ExpeData Data Acquisition & Analysis version 1.1.18, Sable Systems) loaded onto a personal computer.

Body temperature measurements

Body temperature (T_b , °C) of birds was measured throughout metabolic trials using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-118, Physitemp, Clifton, NJ). The thermocouple was inserted into the cloaca of the bird to a depth at which a slight withdrawal did not result in a change in the temperature reading (between 0.5 and 2 cm, depending on the size of the bird, Smit & McKechnie 2010). The thermocouple was secured by attaching the wire to the feathers immediately behind the cloaca, using adhesive tape and a small wire paperclip. Generally, the thermocouple caused no detectable discomfort in the birds and stayed intact throughout the experimental trial. However, some individuals removed the thermocouple with their beaks. The sample size of T_b measurements is thus smaller than for EWL and RMR measurements. Outputs from the thermocouple were digitised using a TC-1000 thermocouple meter (Sable Systems) linked to Expedata software on personal computer.

Experimental protocol

Metabolic measurements using open-flow-through respirometry system

All respirometry experiments were conducted during the day (i.e. sunrise to sunset), which is the active phase of all 12 species involved in this study. Prior to each experiment, birds were weighed to the nearest 0.01 g. Nectarivores (Table 1) were provided with sugar water (25% sucrose solution) directly before the experiment, given the high gut passage rates often observed in these birds (Mbatha et al. 2002). To ensure that the birds' tail feathers did not touch the mineral oil at the bottom of the chamber, the tail feathers of birds with particularly long tails (only certain individuals from Cape Sugarbird, Orange-breasted Sunbird, Malachite Sunbird, Victorin's Warbler, Cape Grassbird and Familiar Chat; scientific names listed in Table 1) were trimmed so that the full downward extension of the shortened tail through the holes in the wire mesh did not reach the oil layer.

After baseline readings were obtained (as described above), each bird was placed individually into a suitably-sized respirometry chamber. The lid of the environmental chamber was closed immediately, creating a darkened environment to minimise distress in the bird. During respirometry experiments, birds experienced a ramped profile of five controlled temperature treatments (starting at a low temperature), each lasting approximately 20-30 min. Air temperature was only increased if the bird remained calm during the test period (assessed using a live video feed together with gas traces, see below). Incremental changes in T_a occurred gradually and typically took about 15 to 20 min for T_a within the chamber to stabilise at the new level (2°-4 °C higher). After each experimental temperature period, reference air was again sub-sampled for at least 5 min.

Monitoring behaviour

Birds were monitored constantly for signs of distress during the trials using a closed-circuit surveillance camera and an infra-red light source inside the environmental chamber. Birds often allow controlled elevations in T_b above normal levels when exposed to heat (Tieleman & Williams 1999; Smit et al. 2013), however lethal T_b in birds (generally from 45° to 47 °C) had to be avoided (Dawson 1954). Therefore, T_b as well as CO_2 , O_2 and H_2O were monitored continually throughout experimental

trials using the Expedata data acquisition software. Concurrently, activity (calm, moving/looking around or jumping) and heat dissipation (panting or wing spreading) behaviours were noted and recorded every 5 min. If birds showed any signs of restlessness that resulted in a sudden increase in T_b (> 43 °C), the trial ceased and the bird was removed from the chamber. Reported values are thus associated with periods of approximately stable RMR and EWL.

Release and/or housing of birds

After the completion of the experimental trial, the temperature was reduced as rapidly as possible to allow the chamber to cool down to approximately room temperature (25 °C). The bird was then removed from the chamber and the thermocouple carefully extracted. The bird was weighed, given water (or sugar water, in the case of nectarivores) to drink and then placed into a cloth bag. Birds were, as far as possible, released directly after trials at the site where they were captured. Birds for which runs finished close to sunset were kept overnight in small shade cloth cages (30x40x50 cm). Cages were placed in a separate, quiet room with room temperature maintained at approximately 25 °C and were protected from noise and other disturbances. Under these circumstances, birds had access to *ad libitum* water and food appropriate to the species (25% sucrose solution for nectarivores, birdseed for granivores, mealworms for insectivores) to ensure they maintained energy and water balance, before being released the following morning at their capture site. Additionally, in the event that more than one bird was captured at the same time, while the first bird was in the respirometry chamber, the others were housed under conditions described above. Birds were held under these circumstances for no more than 48 hours.

Data analysis

Corrections for lag in the O_2 , CO_2 and water vapour measurements, as well as corrections for drift in the O_2 measurements, were made using the appropriate regression analyses in Expedata. VCO_2 was calculated using equation 9.8 in Lighton (2008), which is as follows:

$$VCO_2 = FR_i \{ [F_eCO_2 (1 \delta F_iO_2 \delta F_iCO_2 \delta F_iH_2O) / (1 \delta F_eO_2 \delta F_eCO_2 \delta F_eH_2O)] \delta F_iCO_2 \}$$

VH_2O was calculated using equation 9.9 in Lighton (2008), which is as follows:

$$VH_2O = FR_i \{ [F_eH_2O (1 \delta F_iO_2 \delta F_iCO_2 \delta F_iH_2O) / (1 \delta F_eO_2 \delta F_eCO_2 \delta F_eH_2O)] \delta F_iH_2O \}$$

In the above equations, FR_i = flow rate of nitrogen into chamber; FR_e = flow rate of nitrogen out of chamber; F_iO_2 , F_iCO_2 and F_iH_2O = fractional concentrations of incurrent non-nitrogen gas species; and F_eO_2 , F_eCO_2 and F_eH_2O = fractional concentrations of excurrent non-nitrogen gas species. Due to the large variability of O_2 readings at high flow rates, data from the O_2 analyser was not used to calculate VO_2 . Instead, the respiratory exchange ratio (RER) of each bird was assumed based on its dietary guild and an estimation of the time since its last meal. Nectarivores were assumed to metabolise carbohydrates (RER = 1.00), whereas all other species were assumed to metabolise lipids (RER = 0.71, Walsberg & Wolf 1995). VO_2 was then calculated from the equation $RER = VCO_2/VO_2$ (Walsberg & Wolf 1995). The above VCO_2 and VO_2 values were then used to calculate mass-specific resting metabolic rate (RMR, reported as the rate of metabolic heat production, J/g/h) and VH_2O was used to calculate mass-specific evaporative water loss (EWL, reported as the rate of water vapour production, mg/g/h) using simple energy and mass conversions. In all cases, the lowest 5-10 min mean VCO_2 at each experimental temperature was considered to be indicative of resting values. All VO_2 and VCO_2 values were corrected to STPD (standard temperature, pressure, dry).

Thermal physiological attributes of Blue Hill Nature Reserve species

Data were analysed for normality (Shapiro-Wilks test) and homogeneity (Levene's test) prior to parametric analyses. All statistical analyses were performed in R (R Development Core Team 2013). Davies' tests using the *segmented* package in R (Muggeo 2003) were used to detect changes in the slopes of relationships between EWL, RMR or body temperature (T_b), and air temperature (T_a). Where the Davies' test identified a significant change in a slope, broken stick regression analyses, using the *segmented* package (Muggeo 2003), were used to define the inflection points in T_a above which EWL (inflection point defined as T_{ewl}) and T_b started to increase for each species. Linear mixed-effects regression models, with individual bird as a random factor, were then applied to the data above these inflection points, using the *nlme* package in R (Pinheiro et al. 2013), to determine the rate of change in EWL, RMR and T_b above (or below, where applicable) these inflection points. A general linear model (glm) was used to investigate the relationships between mean onset of panting

temperature (T_{pant}) and T_{ewl} , between T_{pant} and T_{b} inflection point, and between T_{ewl} and T_{b} inflection point. Mean EWL rate, RMR and T_{b} values at 30° and 38 °C were calculated by averaging, for each species, the values of each of these parameters at T_{as} between 29° and 31°C, and 37° and 39 °C, respectively (Appendix A, Table A4). Since values represent only T_{as} at which birds were relatively calm and since each individual did not experience the full range of experimental T_{as} , mean values for the abovementioned parameters do not necessarily include values for each individual per species (Appendix A, Table A4). The change between 30° and 38 °C for each of the abovementioned parameters was calculated by dividing the mean value for each species at 38 °C by that at 30 °C (Appendix A, Table A4).

Interspecific comparison of Blue Hill Nature Reserve species

Both conventional glms and comparative method models (Blomberg et al. 2003) were used to compare the mean inflection points, slopes of lines above inflection points, and absolute values of EWL and T_{b} at 30 °C since this was the air temperature at which most birds showed minimum values for EWL and T_{b} . I also compared the change in EWL and T_{b} between 30° and 38 °C, as the latter was the highest T_{a} shared by all 12 species. In the above analyses I tested for effects of log body mass (log M_{b}), dietary guild (nectarivores, granivores, insectivores), endemism (Fynbos endemics vs. non-endemics, refer to Table 1) and the relative association of each species' range with high temperatures (see maximum entropy analyses below, refer to Appendix B, Table B2). Because of the underlying importance of body mass in explaining physiological traits, I included log M_{b} as a covariate in most models. Due to the small number of species sampled, I tested each of the abovementioned factors in separate models against body mass.

Each species' relative association with high environmental temperatures was extracted from maximum entropy (MaxEnt) model data (A.T.K. Lee and P. Barnard, unpublished data, Appendix B, Table B2). MaxEnt (Phillips et al. 2004) is a spatial modelling programme that uses GPS locations to create a probability surface using (usually) environmental variables such as landscape and climate. MaxEnt is frequently used to map species' geographic distributions (Phillips et al. 2004). For each of the 12 species, probability surfaces were created using 19 climatic variables (from Hijmans et al.

2005). Using Jackknifing and a set-aside test set of the data (20% of positional data locations for each species from A.T.K. Lee and P. Barnard, unpublished data), the contribution of each climatic variable to the probability surface was obtained from the area under the receiver operating characteristics curve (AUC) scores (Elith et al. 2011; Zipkin et al. 2012). The AUC test statistic in MaxEnt is a score of how well a predictive variable accounts for the test positions from the final probability model; the higher the AUC, the more effective the variable (Huang & Ling 2005; Elith et al. 2011). The two variables selected for this comparative analysis were annual mean temperature (ME1) and maximum temperature of the warmest month (ME2), as both were identified by AUC as important for a subset of the species used and are predicted to increase significantly under climate change (Klausmeyer & Shaw 2009). Inspection of species response curves showed that these variables were generally limiting (species present for low values, absent for high values).

Global multispecies comparison

T_{cwl} and the slope of the relationship above this inflection point were compared between species from this study and 33 other species from a variety of additional sources from around the world (Appendix C, Table C1). This comparison was only possible for the above two physiological parameters, because they were the only two that were measured and reported in almost all studies. The 45 species (33 from the literature, 12 from this study) were also grouped, broadly, according to the world climatic zone in which most of their distribution is centered, as classified by W. Köppen in 1900 (updated version: Kottek et al. 2006, Appendix C, Table C1). The classification system is based on vegetation, precipitation and air temperature measures (Kottek et al. 2006). The tropical climatic zone includes species from category A of Köppen's classification i.e. 'equatorial climates', the desert species from category B ('arid climates'), the temperate species from category C ('warm temperate climates') and cosmopolitan species are all species that have distributions in two or more of the abovementioned broad climatic zones.

Phylogenetic analyses

A phylogenetic generalised least-squares (PGLS) analysis using *ape* (Paradis et al. 2004) and *caper* (Orme et al. 2012) packages in R, was performed on the global multispecies dataset, to verify the

outcomes of all conventional glms. PGLS tests take into account that traits may be similar due to relatedness because species with different phylogenetic relationships were compared (Garland & Adolph 1994). One hundred hypothetical phylogenies were sampled for each data set from <http://www.birdtree.org> (Jetz et al. 2012) using the Hackett et al. (2008) phylogeny as backbone. The majority consensus tree identified using the programme Mesquite (Maddison & Maddison 2011) was used.

Initially the models were run with both lambda and kappa branch length transformations and the transformation with the lowest AIC_c (Akaike's Information Criterion with correction for small sample sizes) value was presented for PGLS models. AIC_c values were generally similar ($\hat{\delta} AIC_c < 2$) and models with lambda branch length transformations are presented. Null models of T_{ewl} , log slope of EWL and log M_b from the global analysis were used to establish phylogenetic signal. Phylogenetic signals were detected for log slope of EWL above T_{ewl} ($K = 1.189$, $p = 0.017$) as well as for log M_b ($K = 1.587$, $p < 0.001$), but no signal was detected for T_{ewl} ($K = 0.508$, $p = 0.089$). Phylogenetic signal could not be tested in the BHR data set since there were too few species. Blomberg et al. (2003) suggest > 20 species in data sets to detect phylogenetic signal and to perform accurate branch length transformations. Since I only had 12 species for the BHR analyses, I obtained phylogenetic independent contrasts (PIC) of physiological parameters for these 12 species and performed conventional glm models to account for phylogenetic relatedness.

Model selection and presentation

During analyses, AIC_c values were compared to select the best-fitting model (both conventional, PIC and PGLS models) for each physiological parameter. In cases where AIC_c values were similar ($\hat{\delta} AIC_c < 2$), and models were nested, the simplest model with the least explanatory factors was selected as the best model, following Arnold (2010). In all cases, p values < 0.05 are indicative of significance. All data are mass-specific and are presented as means \pm standard error per individuals measured (n) for each species.

3. Results

Sample sizes

Each individual could only be exposed to a maximum of five experimental temperatures (half of the full temperature regime) during a single respirometry trial, because birds had to remain at each temperature for roughly 30 min, it took 15-20 min for each new temperature to stabilise, and the total length of time spent inside the chamber during a single measurement session could not exceed four hours for ethical reasons. I aimed to run ten individuals per species in order to obtain sufficient data across the full range of temperatures for each species considering the short field season. During the ten week field period, 393 individuals of the 12 target species were captured. 101 of these were successfully processed in the respirometry chamber and data were collected for these individuals.

Thermal physiological attributes of Blue Hill Nature Reserve species

Evaporative water loss

In all 12 species, the rate of mass-specific evaporative water loss (EWL) remained relatively constant at low air temperatures (T_a) up to a certain T_a threshold (T_{ewl}), after which it increased linearly with increasing T_a (Figure 3). T_{ewl} inflection points were statistically significant (i.e. the slopes above and below T_{ewl} were significantly different) for all species, except Victorinø Warbler and Cape Grassbird (Figure 3). Orange-breasted Sunbird had the highest T_{ewl} inflection point ($36.7^\circ \pm 1.0^\circ \text{C}$), which was 5.5°C higher than that of Cape Rockjumper with the lowest inflection point ($31.2^\circ \pm 0.6^\circ \text{C}$). The rate of EWL increase (i.e. the slope of EWL) above T_{ewl} was significantly greater than zero for all species, except Cape Canary where there were too few data above the inflection point to obtain a significant result. The three sunbird species had the steepest slopes above their respective T_{ewl} , averaging a rate of $5.78 \text{ mg/g/h/}^\circ\text{C}$, almost four-fold higher than that of the Cape Rockjumper, which showed the lowest rate of EWL increase above its T_{ewl} ($1.63 \pm 0.13 \text{ mg/g/h/}^\circ\text{C}$, $t = 12.83$, $p = 0$). In addition, Cape Rockjumper had the lowest mean rate of EWL at both 30°C ($3.42 \pm 0.27 \text{ mg/g/h}$) and 38°C ($15.10 \pm 1.14 \text{ mg/g/h}$), but showed the largest relative increase in EWL (4.41-fold increase) between these two air temperatures (Appendix A, Table A4).

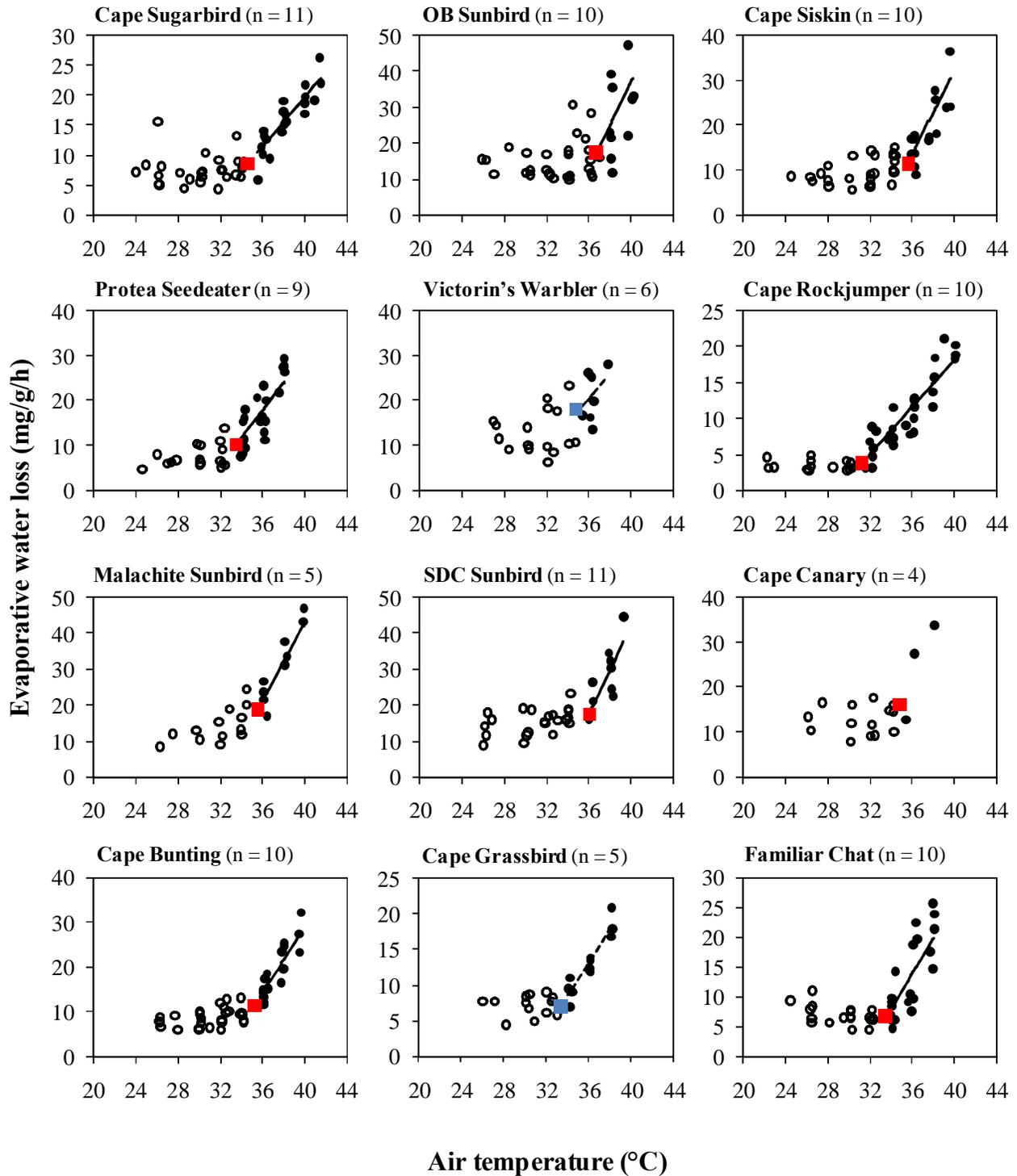


Figure 3. Mass-specific evaporative water loss (EWL, mg/g/h) in all 12 species studied at Blue Hill Nature Reserve over a range of air temperatures (T_a , °C). Segmented regressions were used to estimate the inflection point (T_{ewl} °C), significant = red block, not significant = blue block) in the relationship between EWL and T_a . Data below and above T_{ewl} are indicated by clear and solid circles, respectively. Linear mixed effects regression analyses were performed on data above inflection points. Slopes above significant T_{ewl} are indicated by solid lines. In cases where T_{ewl} was not significant, slopes above this point are indicated by dotted lines. Only significant upper slopes are illustrated.

Resting metabolic rate

Four species (Orange-breasted Sunbird, Victorinø's Warbler, Cape Bunting and Cape Grassbird) showed a significant decreasing trend in mass-specific resting metabolic rate (RMR) across the entire range of air temperatures (T_a) to which they were exposed (Figure 4). Of these four species, Orange-breasted Sunbird had the steepest slope (-3.28 ± 0.64 J/g/h/°C, $t = -5.16$, $p = 0$). Five species had a significant inflection point in the relationship between RMR and T_a (Figure 4). In Cape Sugarbird, RMR decreased at a significant rate of -0.73 ± 0.23 J/g/h/°C ($t = -3.16$, $p = 0.004$) at temperatures above the inflection point ($26.7^\circ \pm 0.6$ °C). In Familiar Chat, RMR decreased significantly (-3.86 ± 0.91 J/g/h/°C, $t = -4.27$, $p = 0.024$) as temperatures increased from the starting temperature to the inflection point at $30.3^\circ \pm 1.6$ °C (Figure 4). Cape Siskin, Southern Double-collared Sunbird and Cape Canary showed no significant change in slope above or below their respective inflection points. RMR appeared to increase above the inflection point (which would be indicative of an upper limit to thermoneutrality) in Southern Double-collared Sunbird, but this was not significant (2.81 ± 1.47 J/g/h/°C, $t = 1.91$, $p = 0.080$). The remaining three species showed no significant relationship between RMR and T_a (Appendix A, Table A2). I therefore could not identify an upper limit to thermoneutrality, using RMR, for any species.

RMR at 30 °C varied between species, as did the response of RMR to increasing T_a . Cape Grassbird had the highest RMR at 30 °C (79.23 ± 1.74 J/g/h) compared to an RMR of 31.79 ± 4.05 J/g/h in Malachite Sunbird, which had the lowest RMR at this T_a (Appendix A, Table A4), while Cape Rockjumper had the lowest RMR at 38 °C (32.15 ± 3.3 J/g/h) and Southern Double-collared Sunbird the highest (96.53 ± 10.01 J/g/h). Four species showed an increase and seven a decrease in RMR between $T_a = 30$ °C and $T_a = 38$ °C (no data available for Cape Canary at 38 °C, Appendix A, Table A4).

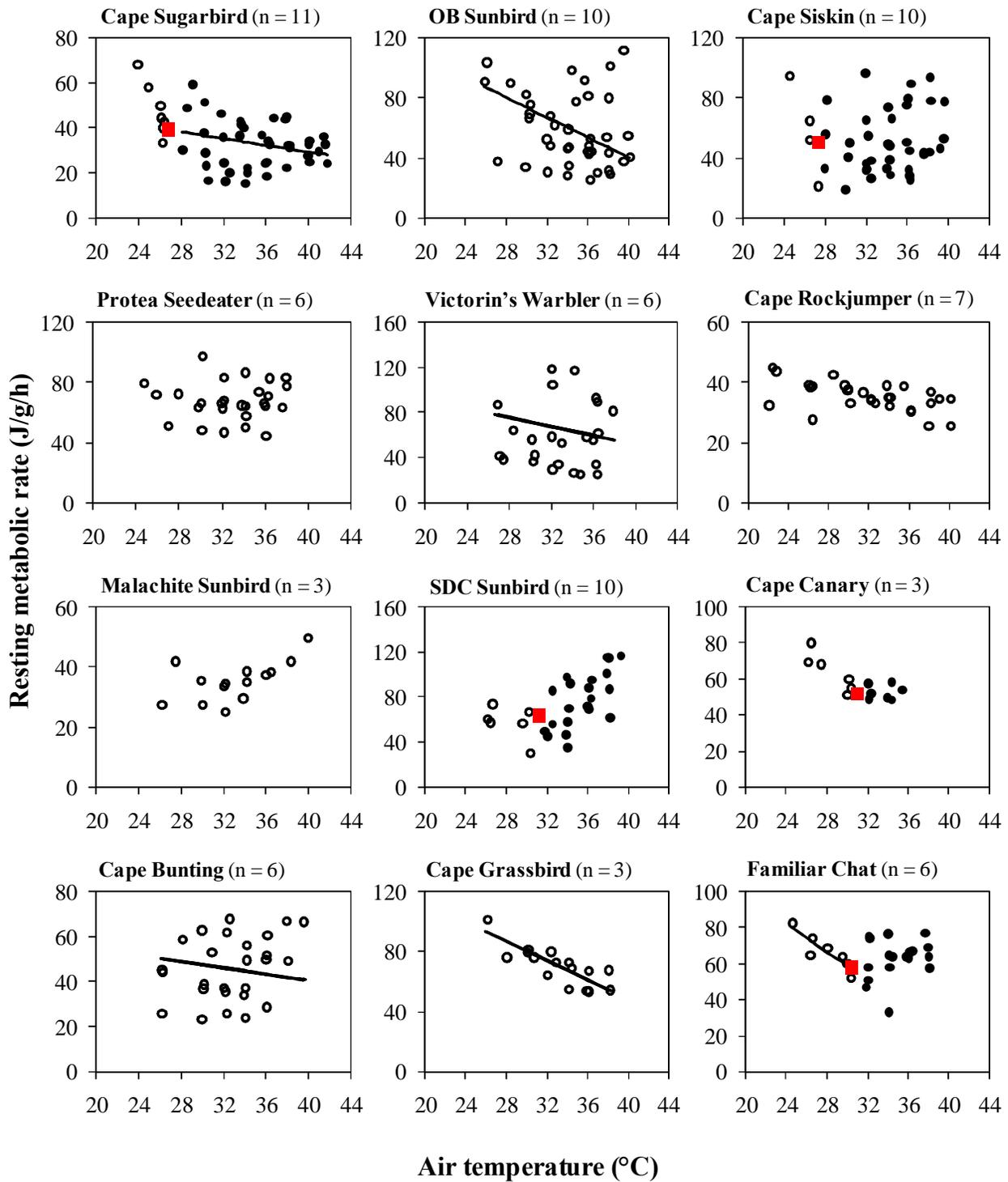


Figure 4. Mass-specific resting metabolic rate (RMR) in all 12 species studied at Blue Hill Nature Reserve over a range of air temperatures (T_a , °C). Conventions as Figure 3, except for the following exceptions: when it was suspected that the inflection point represented a lower, as opposed to a higher, limit of thermoneutrality, slopes below the inflection point are indicated by a solid line. In cases where inflection points were not significant, linear mixed effects regression analyses were performed on the entire dataset for that species and the slope indicated by a solid line.

Body temperature

All species, except Cape Canary, showed an increase in T_b with T_a . Eight species showed a significant inflection point in the relationship between body temperature (T_b) and air temperature (T_a), after which T_b increased significantly at increasing T_a (Figure 5). Of these, Southern Double-collared Sunbird had the highest inflection point ($35.2^\circ \pm 0.6^\circ\text{C}$) as well as the steepest slope above this point ($0.68 \pm 0.09^\circ\text{C } T_b/^\circ\text{C } T_a$, $t = 7.50$, $p = 0.006$). Cape Sugarbird had the lowest inflection point ($30.7^\circ \pm 1.0^\circ\text{C}$), and Cape Grassbird showed the lowest rate of T_b increase above its inflection point (0.25 ± 0.04 , $t = 5.66$, $p = 0.001$). Victorinø Warbler did not show a significant inflection point in the relationship between T_b and T_a , but showed an overall significant increasing trend (0.16 ± 0.04 , $t = 4.30$, $p = 0.001$). Cape Siskin did not have a significant T_b inflection point, although it was near-significant ($p = 0.066$ for Davieø test). The slope of T_b increase at temperatures higher than this point for Cape Siskin was significant (0.17 ± 0.02 , $t = 7.07$, $p = 0$). The two species with low sample size (Malachite Sunbird and Cape Canary) showed no significant relationship between T_b and T_a . Maximum T_b s for individual birds ranged from 40.8°C (in Cape Canary at $T_a = 34.3^\circ\text{C}$) to 43.6°C (in Cape Siskin at $T_a = 38.2^\circ\text{C}$). Mean T_b values across all species ranged from 38.2° to 40.3°C at $T_a = 30^\circ\text{C}$, and from 41.0° to 42.4°C at $T_a = 38^\circ\text{C}$, with all species showing a similar change in T_b between these two air temperatures (between 1.0 and 1.1).

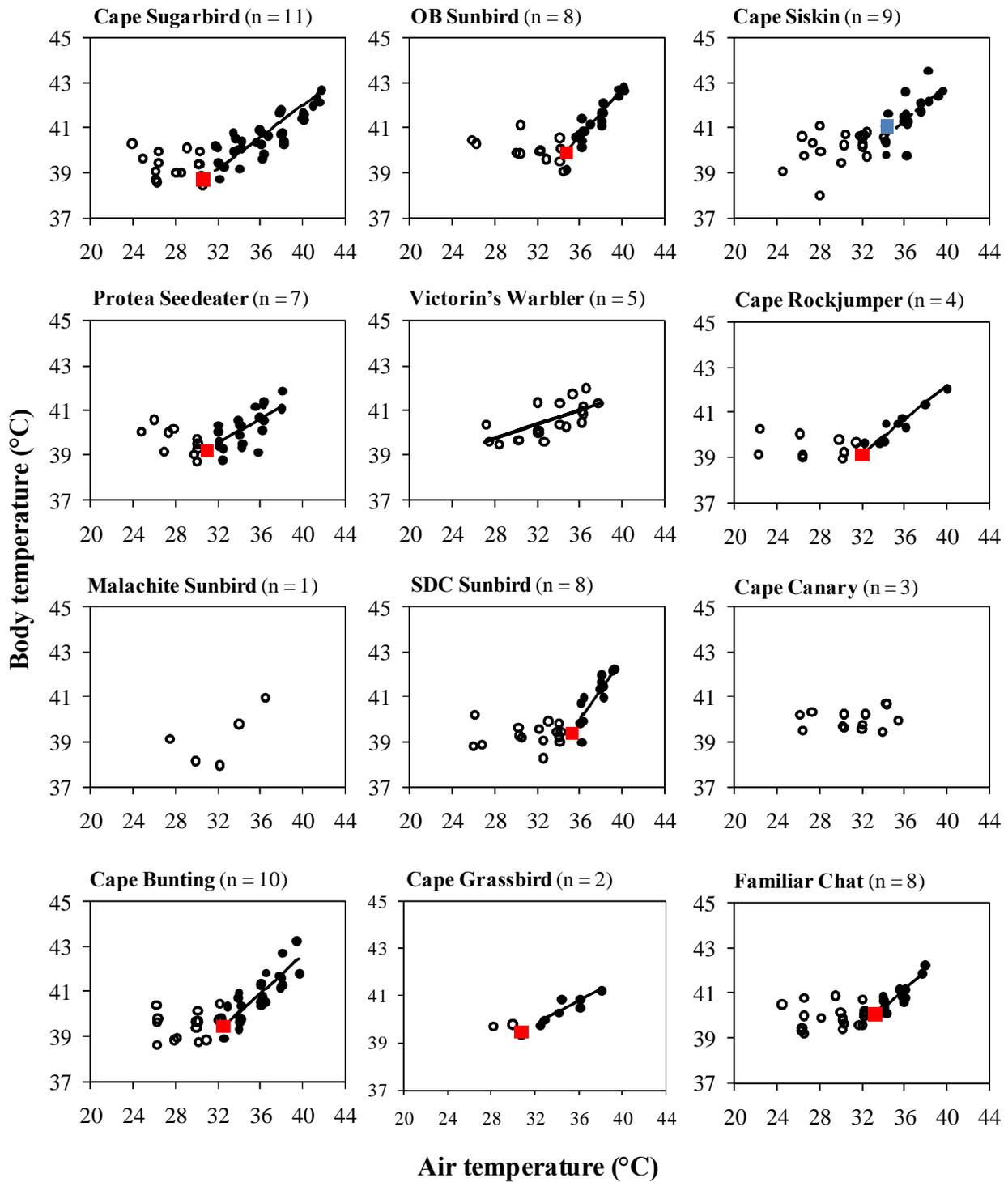


Figure 5. Body temperature (T_b , °C) in all 12 species studied at Blue Hill Nature Reserve over a range of air temperatures (T_a , °C). Conventions as Figure 3, except for the following exceptions: in cases where the inflection point was not significant but there appeared to be an inflection in the data, slopes above the point are indicated by dotted lines. In cases where inflection points were not significant and there appeared to be no inflection in the data, linear mixed effects regression analyses were performed on the entire dataset for that species and the slope indicated by a solid line.

Panting

The mean temperature at which individual birds started to pant (T_{pant}) was $35.1^\circ \pm 0.2^\circ\text{C}$. Orange-breasted Sunbird had the highest mean T_{pant} ($37.8^\circ \pm 0.6^\circ\text{C}$), whereas Cape Rockjumper had the lowest ($33.6^\circ \pm 0.7^\circ\text{C}$) (Table 2). There was a significant positive correlation between T_{pant} and T_{ewl} ($0.65 \pm 0.24^\circ\text{C } T_{\text{pant}}/^\circ\text{C } T_{\text{ewl}}$, $t = 2.77$, $p = 0.020$, Figure 6) and between T_{pant} and T_b ($0.53 \pm 0.15^\circ\text{C } T_{\text{pant}}/^\circ\text{C } T_b$, $t = 3.57$, $p = 0.006$, Figure 7), but not between T_{ewl} and T_b ($t = 1.30$, $p = 0.23$).

Table 2. Mean temperature at which birds started panting ($T_{\text{pant}} \pm \text{Std. Error}$, $^\circ\text{C}$). Table also shows mean EWL inflection point ($T_{\text{ewl}} \pm \text{Std. Error}$, $^\circ\text{C}$), mean T_b inflection point ($T_b \text{ IP} \pm \text{Std. Error}$, $^\circ\text{C}$), total sample size (N total) and the number of individuals that panted (N pant) for each of the 12 species at Blue Hill Nature Reserve.

Species	N total	N pant	Mean T_{pant} (\pm Std. Error, $^\circ\text{C}$)	Mean T_{ewl} (\pm Std. Error, $^\circ\text{C}$)	Mean $T_b \text{ IP}$ (\pm Std. Error, $^\circ\text{C}$)
Cape Sugarbird	11	11	35.2 ± 0.3	34.6 ± 0.6	30.7 ± 1.0
Orange-breasted Sunbird	10	6	37.8 ± 0.6	36.7 ± 1.0	34.7 ± 0.4
Cape Siskin	10	8	35.8 ± 0.5	35.6 ± 0.5	34.3 ± 1.3
Protea Seedeater	9	9	33.8 ± 0.1	33.5 ± 0.6	30.9 ± 0.9
Victorin's Warbler	6	6	33.9 ± 0.4	34.7 ± 1.1	27.5 ± 0.2
Cape Rockjumper	10	8	33.6 ± 0.7	31.2 ± 0.6	32.1 ± 0.8
Malachite Sunbird	5	4	35.8 ± 0.2	35.5 ± 0.6	NA
Southern Double-collared Sunbird	11	5	37.2 ± 0.5	36.0 ± 0.5	36.2 ± 0.6
Cape Canary	4	1	34.1 (NA)	34.9 ± 0.6	31.8 ± 2.7
Cape Bunting	10	8	34.5 ± 0.7	35.3 ± 0.4	32.6 ± 0.9
Cape Grassbird	5	5	34.1 ± 0.4	33.4 ± 1.4	30.8 ± 0.9
Familiar Chat	10	6	36.5 ± 0.2	33.5 ± 0.5	33.3 ± 0.7

NA = not applicable, too few data points

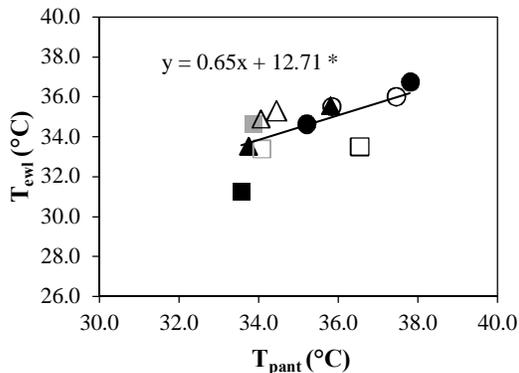


Figure 6. Positive correlation between mean onset of panting temperature (T_{pant} , $^\circ\text{C}$) and mean inflection point in the relationship between air temperature and evaporative water loss (T_{ewl} , $^\circ\text{C}$). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic; black = significant inflection point; grey = non-significant inflection point.

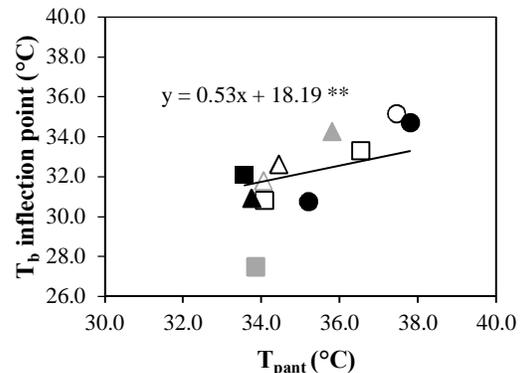


Figure 7. Positive correlation between mean onset of panting temperature (T_{pant} , $^\circ\text{C}$) and mean inflection point in the relationship between air temperature and body temperature (T_b , $^\circ\text{C}$). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic; black = significant inflection point; grey = non-significant inflection point.

Interspecific comparison of Blue Hill Nature Reserve species

All general linear models (both conventional and phylogenetic independent contrast (PIC) models) used to compare eight physiological parameters between the 12 species at Blue Hill Nature Reserve are illustrated in Figure 8, and details of the best model selected for each parameter are shown in Appendix B, Table B3. Data for body mass (M_b) and the slope above the EWL inflection point (T_{ewl}) were log-transformed.

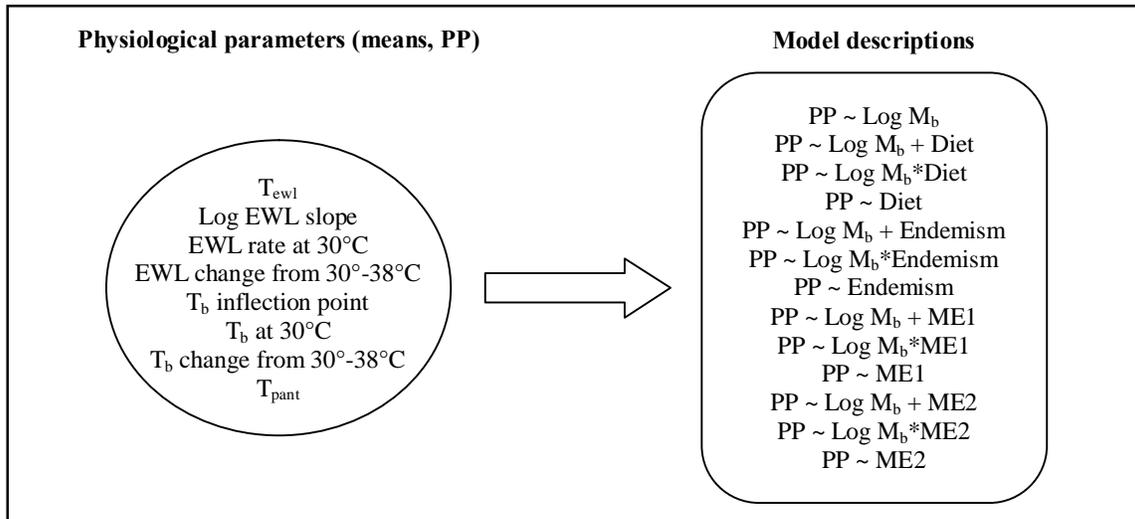


Figure 8. Model descriptions for the 13 general linear models and PIC models run for each of the eight physiological parameters (means, PP) compared between the 12 species at Blue Hill Nature Reserve, Western Cape, South Africa. Each PP (in the left-hand bubble) was used as the response variable for each of the models in the right-hand bubble. T_{ewl} = inflection point in the relationship between air temperature (T_a) and evaporative water loss (EWL); T_b = body temperature; T_{pant} = T_a at which bird started to pant; M_b = body mass; ME1 = MaxEnt 1, annual mean temperature; ME2 = MaxEnt 2, maximum temperature of the warmest month; Endemism = Fynbos endemic, non-endemic; Diet = nectarivore, granivore, insectivore.

Log body mass ($\log M_b$) was selected as the best predictor of T_{ewl} (Figure 9), \log EWL slope (Figure 10), T_b inflection point (Figure 11) and T_{pant} (Figure 12), and was a significant predictor for all the other abovementioned physiological parameters (PP, Appendix B, Tables B3 and B4). All relationships between PP and $\log M_b$ were negative, i.e. smaller species tended to have higher mean T_{ewl} , T_b inflection point and T_{pant} values, as well as steeper EWL slopes, than larger species. All of the abovementioned results from conventional models were supported by PIC analyses, except in the case of the T_b inflection point where the significant effect of $\log M_b$ disappeared after accounting for phylogeny ($\log M_b$, $t = 0.74$, $p = 0.482$). AIC_c values for the three best-fitting conventional models for

T_b at 30 °C did not differ by more than 2 units and neither of the best two models were significant predictors of this PP ($\log M_b$, $t = -0.70$, $p = 0.499$; ME1, $t = 0.15$, $p = 0.882$; Appendix B, Tables B3 and B4). $\log M_b$ was the best predictor of T_b at 30 °C in PIC models, but this was also not significant ($t = -1.82$, $p = 0.102$, Appendix B, Table B4). Figures 9 to 12 illustrate significant conventional model outcomes only.

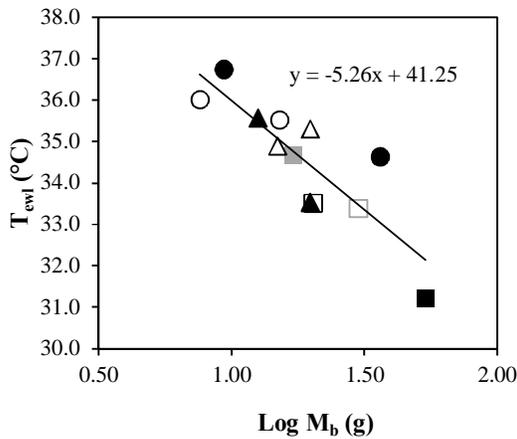


Figure 9. Negative relationship between log mean body mass ($\log M_b$, g) and the mean inflection point in the relationship between air temperature and evaporative water loss (T_{ewi} , °C). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic; black = significant inflection point; grey = non-significant inflection point.

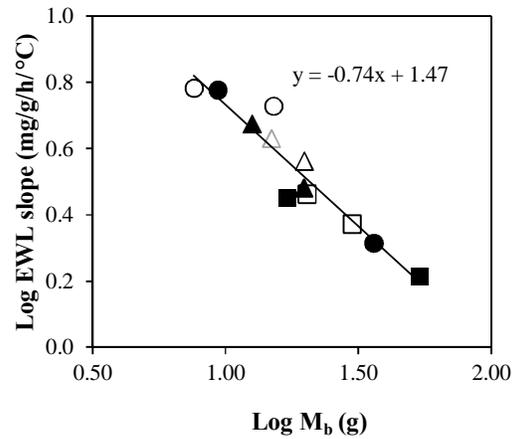


Figure 10. Negative relationship between log mean body mass ($\log M_b$, g) and mean log slope of evaporative water loss above T_{ewi} ($\log EWL$ slope, mg/g/h/°C). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic; black = significant slope; grey = non-significant slope.

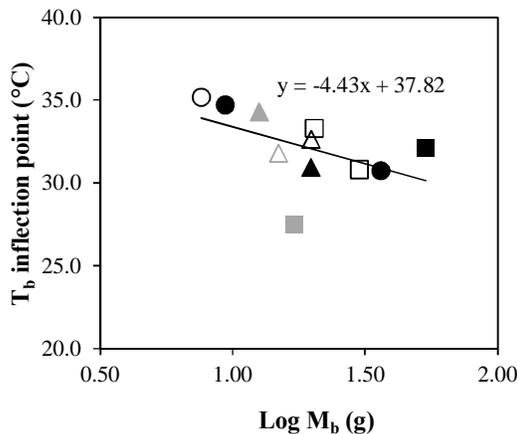


Figure 11. Negative relationship between log mean body mass ($\log M_b$, g) and the mean inflection point in the relationship between air temperature and body temperature (T_b inflection point, °C). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic; black = significant inflection point; grey = non-significant

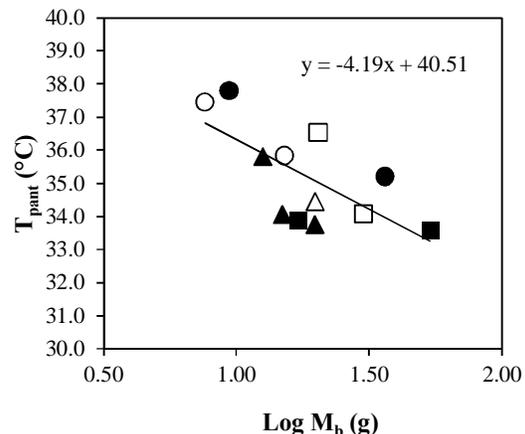


Figure 12. Negative relationship between log mean body mass ($\log M_b$, g) and the mean air temperature at which birds started to pant (T_{pant} , °C). Each point represents a species tested. Circles = nectarivores; triangles = granivores; squares = insectivores; solid = Fynbos endemic; open = non-endemic.

In conventional analyses, the rate of EWL at 30 °C was best explained by the interaction between log M_b and the degree to which the species' range is limited by annual mean temperature (ME1), according to MaxEnt model data (log M_b *ME1, $t = 3.44$, $p = 0.009$, Figure 13). There was no correlation between log M_b and ME1 ($r = 0.058$, $p = 0.092$). Log M_b and ME1 therefore each have an independent, but also an interacting effect on the rate of EWL at 30 °C, i.e. ME1 had a greater effect on EWL rate at 30 °C in larger species and a weaker effect in smaller species (Appendix B, Table B4). However, the interaction was not important after accounting for phylogeny in PIC analyses (Figure 14, Appendix B, Table B3). Here the best model was $EWL_{30} \sim \text{Log } M_b + \text{ME1}$, where each explanatory variable independently showed a significant negative relationship with EWL at 30 °C (log M_b , $t = -5.32$, $p = 0.001$; ME1, $t = -5.85$, $p = 0.000$, Appendix B, Table B4). For example, Cape Rockjumper, which is the largest species (mean $M_b = 53.71 \pm 1.52$ g) and has the most temperature-limited range according to MaxEnt data (ME1 AUC = 0.85), had the lowest rate of EWL at 30 °C (3.42 ± 0.27 mg/g/h). Conversely, Southern Double-collared Sunbird, which is the smallest species (mean $M_b = 7.61 \pm 0.25$ g) and has one of the least temperature-limited ranges (ME1 AUC = 0.59), had the highest rate of EWL at 30 °C (14.17 ± 1.90 mg/g/h).

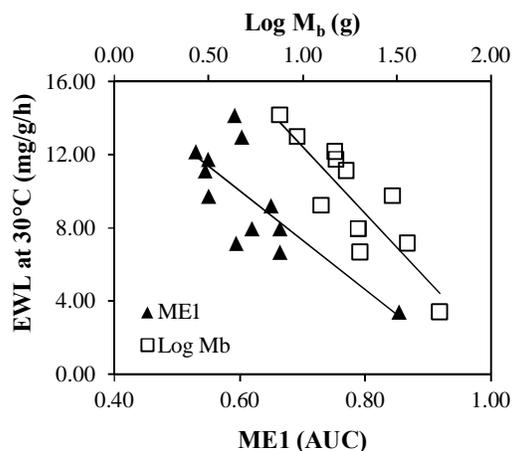


Figure 13. Conventional model outputs showing negative relationships between log mean body mass (Log M_b) and the rate of evaporative water loss (EWL) at 30°C ($t = -4.43$, $p = 0.002$), and between AUC values for MaxEnt models predicting relative correlations between species' ranges and annual mean temperature (ME1), and EWL rate at 30°C ($t = -4.21$, $p = 0.003$). In addition to these significant independent effects, there was a significant interaction between log M_b and ME1 ($t = 3.44$, $p = 0.009$).

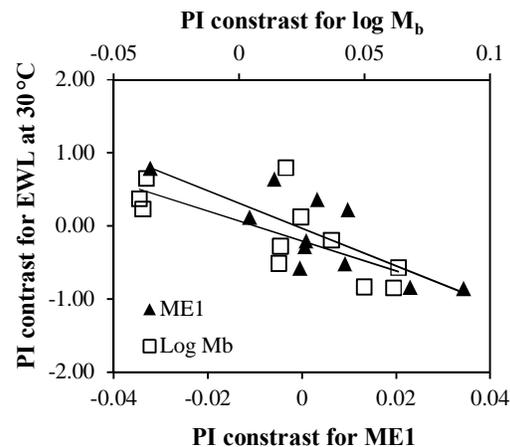


Figure 14. Phylogenetic independent (PI) contrasts for the relationships between log mean body mass (Log M_b) and the rate of evaporative water loss (EWL) at 30°C ($t = -5.32$, $p = 0.001$), and between AUC values for MaxEnt models predicting relative correlations between species' ranges and annual mean temperature (ME1), and EWL rate at 30°C ($t = -5.85$, $p = 0.000$). While the independent effects of each of the abovementioned factors remained after accounting for phylogeny, the significant interaction between log M_b and ME1 was lost.

The change in EWL between 30° and 38 °C was best explained by ME1, independent of log M_b , in conventional models. Those species that are more limited by annual mean temperature (ME1), such as Cape Rockjumper and Protea Seedeater, experienced a significantly greater change in EWL between 30° and 38 °C ($t = 3.61$, $p = 0.005$) than species like Cape Canary and Victorinø Warbler which are less limited by ME1 (Figure 15, Appendix B, Tables B2 and B4). However, this correlation with ME1 disappeared once phylogeny was taken into account; log M_b was the best predictor of the change in EWL between 30° and 38 °C in the PIC analysis ($t = 2.46$, $p = 0.036$, Figure 16, Appendix B, Table B4).

AIC_c values for the three best-fitting conventional models investigating the change in T_b between 30° and 38 °C did not differ and neither of the best two factors was a significant predictor of this parameter (ME1, $t = 1.30$, $p = 0.230$; ME2, $t = -0.05$, $p = 0.958$; Appendix B, Tables B3 and B4). This was similar for PIC model outcomes (ME1, $t = 0.76$, $p = 0.473$; Log M_b , $t = -0.42$, $p = 0.686$; Appendix B, Tables B3 and B4).

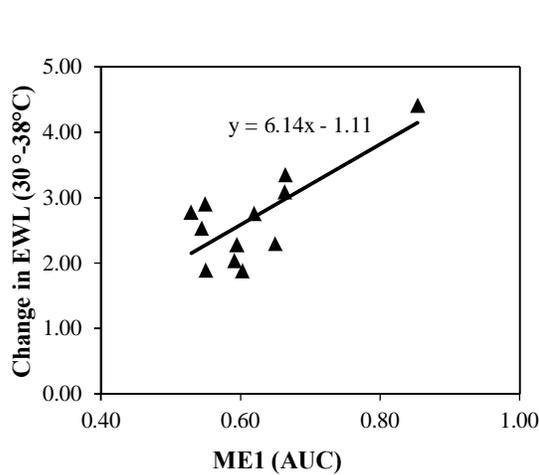


Figure 15. Conventional model output showing significant positive relationship between AUC values for MaxEnt models predicting relative correlations between speciesø ranges and annual mean temperature (ME1), and the change in evaporative water loss (EWL) between 30° and 38°C ($t = 3.61$, $p = 0.005$).

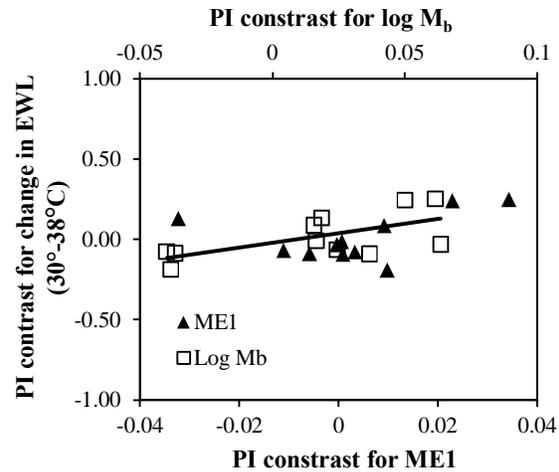


Figure 16. Phylogenetic independent (PI) contrasts for the relationship between log mean body mass (Log M_b) and the change in EWL between 30° and 38°C (black line, $t = 2.46$, $p = 0.036$). The previously significant relationship between AUC values for MaxEnt models predicting relative correlations between speciesø ranges and annual mean temperature (ME1), and the change in EWL is not significant after accounting for phylogeny in the PIC model.

Dietary guild, endemism status and MaxEnt 2 (ME2, maximum temperature of warmest month) did not explain any of the parameters better than M_b or ME1, and are thus less important in explaining the variation in physiological responses between the 12 bird species (Appendix B, Table B3).

Global multispecies comparison

In conventional analyses of the Fynbos species from this study and 33 other species from additional sources (Appendix C, Table C1), log body mass (log M_b) and study (i.e. BHNR or other) were the most important predictors of T_{ewl} (Appendix C, Table C2). BHNR birds showed significantly lower T_{ewl} values as a function of log M_b compared to birds from other regions ($t = 4.50, p < 0.001$, Figure 17, Appendix C, Table C3). The PGLS analyses corroborated these findings ($t = 3.25, p = 0.002$, Appendix C, Table C3). Across all studies, log M_b was the most important predictor of log slope of EWL above T_{ewl} in both conventional and PGLS analyses (Appendix C, Table C2). The slope showed a significant negative relationship to log M_b in both analyses ($t = -16.50, p < 0.001$ for conventional analysis; $t = -9.60, p < 0.001$ for PGLS analysis; Appendix C, Table C3), but did not differ significantly between species from different data sources (Figure 18, Appendix C, Table C3). Figures presented below represent only conventional model outcomes.

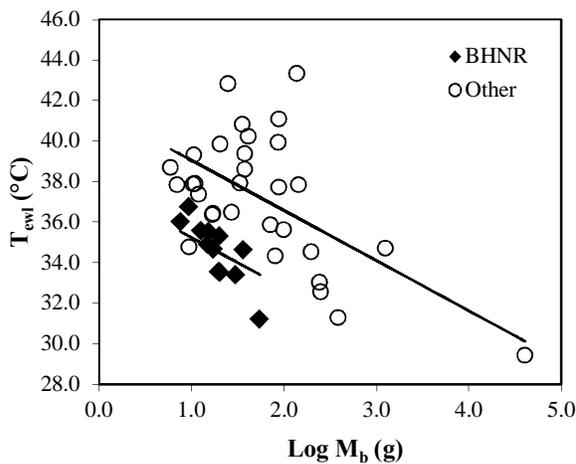


Figure 17. The relationship between log mean body mass (Log M_b , g) and mean EWL inflection point (T_{ewl} , °C) for both Blue Hill Nature Reserve (BHNR) species and species from other regions of the world. BHNR species had significantly lower mean T_{ewl} values compared to species from elsewhere.

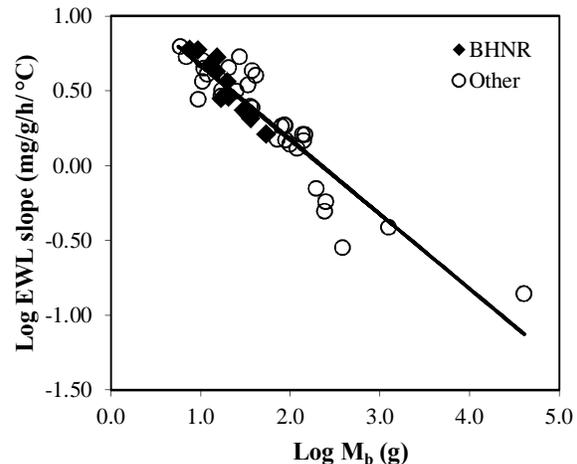


Figure 18. Log mean slope (Log EWL slope, mg/g/h/°C) of the line above the evaporative water loss inflection point decreased significantly with increasing log mean body mass (Log M_b , g) in both Blue Hill Nature Reserve (BHNR) species and species from other regions. In addition, there was no significant difference in this relationship between BHNR and other species. This figure shows a pooled trendline through both datasets using coefficients

I also investigated whether the interspecific patterns of T_{ewl} and the slope of EWL above T_{ewl} might be explained by the world climatic zone (following broad classifications in Kottek et al. 2006, Appendix C, Table C1) in which the majority of the species distribution is centered. In both conventional and PGLS analyses, T_{ewl} was best explained by $\log M_b$ and climate zone (Appendix C, Table C2). T_{ewl} as a function of $\log M_b$ was significantly higher in desert-dwelling species compared to species from other climatic zones ($t = 3.18$, $p = 0.003$, Appendix C, Table C3) and was lowest in temperate species (Figure 19, Appendix C, Table C3). This pattern remained significant after phylogeny was taken into account ($t_{5,38} = 2.52$, $p = 0.016$ for desert birds, Appendix C, Table C3). $\log M_b$ was the best predictor of the log slopes of EWL relationships above T_{ewl} in both conventional (-0.50 ± 0.03 , $t = -16.50$, $p < 0.001$) and PGLS (-0.43 ± 0.04 , $t_{2,43} = -9.60$, $p < 0.001$) analyses (Figure 20, Appendix C, Table C3). The slope of EWL above T_{ewl} was thus independent of the broad world climatic zone in which the species was classified.

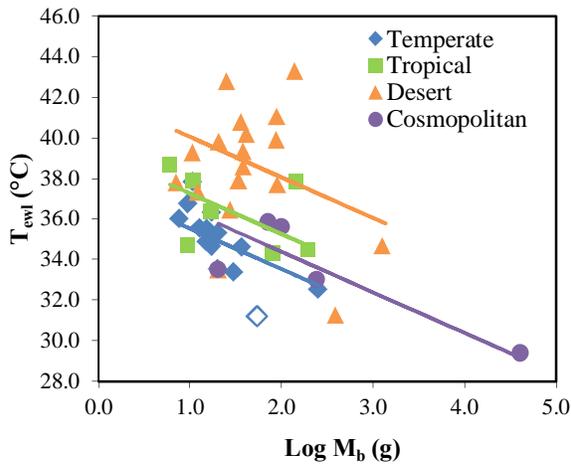


Figure 19. Species from all climatic zones showed a decreasing trend in the relationship between log mean body mass ($\log M_b$, g) and mean EWL inflection point (T_{ewl} , °C). Desert species had significantly higher mean T_{ewl} values compared to species from other climatic zones and temperate species had the lowest mean T_{ewl} values. Clear blue diamond = Cape Rockjumper, highlighting its much lower T_{ewl} for its body size

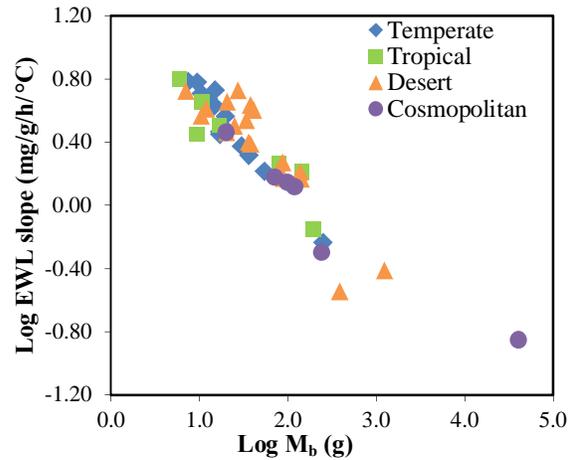


Figure 20. Log mean slope of the line above T_{ewl} (Log EWL slope, mg/g/h/°C) showed a similar decreasing trend with increasing log mean body mass ($\log M_b$, g) in species from all four broad world climatic zones.

4. Discussion

This is the first study of the physiological responses to high temperatures of passerine bird species in the Fynbos biome, South Africa. The strong effect of body mass on the EWL responses of 12 Fynbos bird species supports predictions made by similar studies (Bartholomew & Cade 1963; Austin 1976; Stevenson & Bryant 2000; McKechnie & Wolf 2010) and has possible implications for how different Fynbos birds might respond to climate warming. A large proportion of avian thermal physiology literature is based on desert-dwelling species (e.g. Bartholomew et al. 1962; Hinds & Calder 1973; Ward & Pinshow 1995; McKechnie & Lovegrove 2003; Smit et al. 2013). My results add to the current literature on the topic and specifically increase knowledge on thermal tolerances of birds in a temperate climatic zone, for which data are generally lacking.

Evaporative water loss and panting

All 12 Fynbos species started panting to facilitate evaporative cooling as the air temperature (T_a) increased in the respirometry chamber. It is thus likely that these birds will also have to increase their expenditure of time and water on thermoregulation in future, as air temperatures in the Fynbos biome rise due to climate change (Tieleman & Williams 2002b; du Plessis et al. 2012).

EWL and panting thresholds

For all species, the rate of mass-specific evaporative water loss (EWL) remained relatively constant at low $T_{a,s}$ (ranging from 22.2° to 31.2 °C) up to a certain threshold temperature (T_{ewl}), after which it increased linearly with T_a . Similar patterns have been observed in numerous other studies on birds (Collins et al. 1980; Wolf & Walsberg 1996a; Tieleman et al. 2002) and mammals (Cory Toussaint & McKechnie 2012). This non-linear pattern of EWL is in agreement with the classic model of endothermy (Scholander et al. 1950), which predicts that animals should expend increasing amounts of energy and water in order to regulate T_b at temperatures above the thermal neutral zone (TNZ).

Birds that started increasing EWL at lower T_a generally showed a more gradual rate of increase above T_{ewl} , which supports the findings of previous studies on birds (see McKechnie & Wolf 2010) and bats (Cory Toussaint & McKechnie 2012). Interspecific variation in the T_a at which panting was initiated (T_{pant}), T_{ewl} and the rate at which EWL increased at temperatures above T_{ewl} , was best explained by the variation in body mass (M_b) between species; the species in this study spanned a sevenfold range of mean M_b (from 7.6 g to 53.7 g). In general, the larger species started panting and increasing EWL at lower temperatures than the smaller species, but showed a more gradual increase in EWL at higher T_a . A similar pattern was observed in numerous other studies (Bartholomew & Cade 1963; Austin 1976; Stevenson & Bryant 2000; McKechnie & Wolf 2010). For example, in my study the two smallest species (Southern Double-collared Sunbird (7.6 ± 0.2 g) and Orange-breasted Sunbird (9.2 ± 0.4 g)) only started panting when $T_a > 37$ °C and started increasing EWL above baseline levels when $T_a > 36$ °C, but EWL increased relatively quickly thereafter (at a rate of about 6.00 mg/g/h/°C). These T_{ewl} inflection points are similar to those reported by other researchers for birds of this size. For example, Black-rumped Waxbill (*Estrilda troglodytes*), which weighs 6-7 g, started increasing EWL at $T_a > 35$ °C (Lasiewski et al. 1964) and Verdin (*Auriparus flaviceps*), which weighs roughly 7.0 g, increased EWL from $T_a > 36$ °C (Wolf & Walsberg 1996a). In contrast, Cape Rockjumper, the largest Fynbos species studied, had a mean T_{ewl} nearly 5 °C lower (31.2 °C) and a post-inflection point rate of EWL increase approximately four-fold lower (1.63 mg/g/h/°C) than that of the two small sunbirds.

The strong effect of body mass on interspecific patterns of EWL reflects the importance of body size for the energy and water requirements of thermoregulation (Scholander et al. 1950; Porter & Kearney 2009; McKechnie & Wolf 2010), which in turn could influence species range sizes (Gaston & Blackburn 1996), abundances (Lewis et al. 2008) and life history strategies (Rohwer et al. 2009). Birds need to be able to maintain water balance while simultaneously thermoregulating to maintain a constant body temperature (Austin 1976). Larger birds have smaller surface area-to-volume ratios (Austin 1976) and consequently lower mass-specific rates of EWL (Schmidt-Nielsen 1984; Stevenson & Bryant 2000). This has opposing physiological costs and benefits. Low EWL in larger birds means less water is lost, reducing the risk of dehydration at high temperatures (Weathers 1981; Tieleman &

Williams 1999; McKechnie & Wolf 2010). However, large birds are likely to experience a lower efficiency of evaporative heat loss and have a higher thermal inertia, and thus experience greater costs of avoiding lethal hyperthermia at high $T_{a,s}$ (McKechnie & Wolf 2010).

Bartholomew & Cade (1963) showed that maintaining water balance is most costly for birds weighing less than 50 g as a result of high mass-specific rates of EWL. This includes all of the species I studied except Cape Rockjumper, which has a mean M_b of 53.7 g. The low mean T_{ewl} of Cape Rockjumper indicates that individuals of this species started increasing EWL once $T_a = 31.2$ °C and thus increased mass-specific EWL nearly four times between 30° and 38 °C. Smaller species on the other hand only doubled EWL between these two temperatures, because they started to increase EWL at higher $T_{a,s}$. These findings are comparable to those of other studies on similar sized birds (Lasiewski et al. 1964). However, given their generally rapid increases in water loss at $T_{a,s}$ exceeding T_{ewl} , smaller species such as Malachite Sunbird were already losing more than 3% M_b per hour due to EWL at 38 °C. In contrast, Cape Rockjumper which initiated EWL at lower T_a , was only losing 1.5% body mass per hour at 38 °C.

At moderate T_a , EWL can account for up to 83% of total water loss in small birds (Willoughby 1968; Bartholomew 1972; Williams 1996). According to McKechnie & Wolf (2004), it is not only the quantity of water lost via evaporation that is important, but also the route by which this water is lost. In this study, I measured total evaporative water loss, which comprises both cutaneous (CEWL) and respiratory (REWL) EWL components (Tieleman et al. 2002). In most bird species studied to date, CEWL represents roughly 40-75% of total EWL at moderate air temperatures (Lasiewski et al. 1971; Dawson 1982; Webster & King 1987; Wolf & Walsberg 1996a; Tieleman & Williams 2002a; McKechnie & Wolf 2004; Ro & Williams 2010). In passerine birds, the relative contribution of REWL increases with air temperature (Dawson 1982; Wolf & Walsberg 1996a; Tieleman & Williams 2002a) and becomes the primary mode of heat dissipation during heat stress (Wolf & Walsberg 1996a). McKechnie & Wolf (2004) suggested that reliance on REWL may be more energetically costly than CEWL; therefore, having the ability to delay the onset of increasing REWL at high $T_{a,s}$ (as was perhaps evident in smaller species with higher $T_{ewl,s}$) may be beneficial. This suggests that larger

passerine birds may face a greater cost at higher temperatures, due to the onset of increased EWL at lower air temperatures.

Wing spreading behaviour as a means of heat dissipation was also observed in many individuals, but this measure could not be quantified accurately because it was often difficult to distinguish wing spreading from normal behaviour on the video camera. Wing spreading could facilitate CEWL and passive heat loss (Smit et al. 2013) and therefore warrants further study.

Interspecific variation in EWL at 30 °C

After accounting for phylogenetic relatedness, both M_b and MaxEnt model estimates of the degree to which the species' range is limited by annual mean temperature (ME1; A. T. K. Lee and P. Barnard, unpublished data) were important predictors of the interspecific variation in mass-specific EWL at 30 °C. In general, larger species (such as Cape Rockjumper and Cape Sugarbird) as well as species with ranges showing strong correlation with annual mean temperature (such as Cape Rockjumper, Protea Seedeater, Cape Siskin and Familiar Chat) had lower mass-specific EWL rates at 30 °C than smaller and less ME1-limited species (such as the sunbirds). The fact that mass-specific EWL at 30 °C was lower in larger species is not surprising, given their smaller surface area-to-volume ratios (see above). However, it is interesting that species associated with cooler climates generally had lower rates of EWL at 30 °C compared to those associated with warmer climatic regions. The majority of the Fynbos biome falls within a winter rainfall region where relatively arid conditions prevail during summer (Cowling et al. 1999; Midgley et al. 2003). Since this study was conducted during early summer in the Fynbos biome at a site with a mean annual rainfall of less than 400 mm (Lee & Barnard 2013), the relatively dry conditions may have selected for lower basal EWL in some of these range-limited species. This is in line with predictions by Williams (1996) and Tieleman et al. (2002) that EWL should be lower in arid regions where water may be limiting, as an adaptation to minimise water loss and reduce the risk of dehydration.

My results may be skewed by the Cape Rockjumper, which is much larger than the other species in my study (on average, nearly 20 g heavier than the second largest species, Cape Sugarbird), and has a

ME1 AUC score of 0.85, suggesting that its distribution shows a high degree of correlation to annual mean temperature (other species' ME1 scores ranged from 0.53 to 0.66). The Cape Rockjumper thus emerges as an outlier both in terms of body size and preference for regions with cooler annual mean temperatures. The species is a high altitude specialist with ranges that are restricted to mountain slopes and peaks (Hockey et al. 2005) where air temperatures are generally cooler than surrounding lower-lying regions. In order to draw more accurate conclusions about the vulnerability of Cape Rockjumper relative to the other Fynbos species, a larger sample size of species is required. This should include more bird species of similar size to Cape Rockjumper with ranges in the Fynbos biome, but which are not necessarily restricted to cool highlands (e.g. Bokmakierie (*Telophorus zeylonus*), Cape Rock Thrush (*Monticola rupestris*) and Sentinel Rock Thrush (*M. explorator*)).

Behavioural thermoregulation in Fynbos birds

Air temperatures in the Fynbos biome are currently rising due to climate change (Midgley et al. 2003). In light of this, it is important to consider a bird's capacity for behavioural as well as physiological thermoregulation. Behavioural thermoregulatory strategies may also be influenced by body size.

As air temperatures increase, birds select cooler microhabitats, such as shaded areas under trees or underground burrows of small mammals (Ricklefs & Hainsworth 1968; Williams et al. 1999). This refuge-seeking behaviour delays the onset of excessive water loss via evaporative cooling (Ricklefs & Hainsworth 1968; Barrows 1981; Walsberg 1993; Wolf & Walsberg 1996b). For example, birds retreating to shaded microsites have been shown to save more than 50% water (Barrows 1981; Wolf & Walsberg 1996b). Victorin's Warbler, which utilises the shaded scrub undercanopy (Hockey et al. 2005), may thus through its behaviour have a significant buffer to temperatures experienced in the overstory.

Birds may also reduce activity at high temperatures in an attempt to lower metabolic heat loads (Ricklefs & Hainsworth 1968). But even when inactive and in the shade, small birds can lose 5% M_b per hour via EWL, under very hot conditions (Wolf & Walsberg 1996b). The mass lost will need to be

replaced by consuming more water or, if water is scarce or unavailable, intake of food with high water content must be increased (Cade et al. 1965). This is a problem for granivorous species, such as Cape Siskin and Protea Seed-eater, which have very few options for increasing dietary water intake due to the low water content of most seeds (Bartholomew & Cade 1963). In addition, spending more time thermoregulating at high temperatures is likely to leave less time for foraging (Tieleman & Williams 2002b; Buckley 2008) leading to a decrease in foraging intake (Verbeek 1972; Austin 1976), which may incur significant fitness costs (du Plessis et al. 2012; Cunningham et al. 2013). For species which forage on concentrated food sources within small areas (e.g. Protea flowers or seed sources), this poses less of a problem than for insectivorous species which generally rely on a diffuse food source.

In a behavioural study of birds in southern African deserts, Louw (2011) suggested that small birds (< 150 g) may be less stressed than larger birds (> 150 g) at the same temperature. She proposed that this might be because large species (e.g. Common Ostrich (*Struthio camelus*, mean $M_b = 95$ kg) and bustards (Otididae, mean $M_b > 700$ g, Hockey et al. 2005)) are likely to have fewer cool microsites available to them than smaller birds (an idea supported by Wolf & Walsberg 1996b; and Kearney & Porter 2009). However, although there was wide variation in body size between the Fynbos bird species in my study, all were within Louw's small size category (< 150 g). What may pose more of a problem for these small birds is how species of different body sizes may differ in their use of the landscape as T_a s rise. Shifting microsites, even distances < 1 m, can have considerable effects on thermoregulatory costs faced by different animals (Wolf & Walsberg 1996b). Large birds such as Cape Rockjumpers will most likely have to seek shade earlier than smaller birds and will thus have to spend more time heat dissipating and less time foraging on a daily basis (Lovegrove 1993), because they are less capable of dissipating heat once acquired. Small birds (< 10 g) can easily move in and out of the shade, quickly dumping heat that they pick up when in the sun, and thus might be able to stay active and continue foraging for longer (Austin 1976; B. Smit, unpublished data). Behavioural studies investigating microsite utilisation and changes in activity and foraging patterns of Fynbos bird species as T_a rises are required to support the physiological data from this study.

Resting metabolic rate

The relationship between T_a and resting metabolic rate (RMR) was less clear than for EWL in the 12 Fynbos species. According to the classic model of endotherm energetics proposed by Scholander et al. (1950), endotherms maintain a relatively constant resting metabolic rate at $T_{a,s}$ within the TNZ, but need to increase metabolism at T_a s above this zone to dissipate accumulating heat from the body to the environment (Bartholomew et al. 1962). Since a portion of this heat is due to metabolic processes, a low metabolic rate should be advantageous to the animal as it would reduce the total heat load (Bartholomew et al. 1962). Passerine birds generally have higher metabolic rates than non-passerines of comparable size (Lasiewski & Dawson 1967; Vleck & Vleck 1979) and birds from high altitudes tend to have higher metabolic rates than those acclimated to lower altitudes (Lindsay et al. 2009). The 12 bird species that I studied may thus already be at a disadvantage in light of future climate warming as they are all passerines (Hockey et al. 2005) and the study site is 1 000 to 1 530 m above sea level.

In most study species, RMR decreased as a function of T_a throughout the experimental period and, while five species had significant inflection points in the relationship between T_a and RMR, I could not identify a clear upper critical limit to thermoneutrality in any species. In Southern Double-collared Sunbird, RMR increased relatively rapidly after the inflection point, which may be indicative of an upper critical limit to TNZ at 31.2 °C. However, this increase was not significant most likely due to the small sample size, large variation amongst individuals or an increase in activity observed in many of the birds at higher temperatures. On the other hand, the RMR pattern in the Familiar Chat was possibly indicative of a lower critical limit to thermoneutrality at 30.3 °C; however, this requires further investigation with a larger sample size.

The efficiency of thermoregulation cannot be derived based solely on the amount of water evaporated at any given T_a , since any heat lost needs to be balanced by heat production via metabolism (Lasiewski & Seymour 1972). Given that small birds generally have higher metabolic rates than larger birds (Lasiewski & Seymour 1972), the higher mass-specific EWL rates observed in small birds in my study might not reflect more effective EWL, but rather higher metabolic expenditures. Due to my

incomplete set of results for RMR (see below), I could not calculate thermoregulation efficiency, but this should certainly be explored in future studies.

There are numerous limitations to the RMR data set in this study. First, some individuals were very restless inside the respirometry chamber and usable metabolic data for those birds are thus limited. While all data used in the study represent periods when birds were relatively calm, metabolic values may be slightly higher for individuals that were particularly active during the experiment as they may not have reached an entirely rested state. Moreover, there was considerable intraspecific variation in the activity levels of birds in the chamber, possibly explaining the high error in certain species' RMR data sets (e.g. Orange-breasted Sunbird, Cape Siskin, Cape Bunting). Animals were also most likely stressed due to the capturing and handling process. Handling stress in experimental set-ups is known to increase the metabolic rate of animals (e.g. Davis & Schreck 1997), possibly confounding these data. These limitations shed light on the possible reasons for the general lack of significant RMR trends observed in my study and necessitate further investigation using a larger sample size.

Body temperature

In general, my 12 study species showed an increase in body temperature (T_b) as T_a increased. Eight of the 12 species showed a significant inflection point in the relationship between T_b and T_a , above which T_b increased more rapidly. Body mass may again explain this pattern, with larger species such as Cape Sugarbird and Cape Grassbird increasing T_b at lower T_a s (30.7° C and 30.8 °C, respectively), but at a more gradual rate than smaller species like Southern Double-collared Sunbird (T_b inflection point = 35.2 °C). This is similar to what Cory Toussaint & McKechnie (2012) observed in bats. However, this M_b effect did not hold true after accounting for phylogeny. In addition, there was no significant interspecific variation in T_b values at 30 °C. All species seemed to show a similar change in T_b (on average 1.3° to 2.3 °C increase) as T_a increased from 30° to 38 °C, which is similar to what was found in free-living desert birds by Smit et al. (2013).

My results suggest that all species employed facultative hyperthermia at high temperatures. In general, the increase in T_b occurred before the increase in panting (on average, 3.0 °C below T_{pant}) and EWL (on average, 2.6 °C below T_{ewl}), suggesting that facultative hyperthermia was an initial response to increasing T_a , prior to employing evaporative cooling mechanisms.

Birds often employ facultative hyperthermia by increasing T_b 2° to 4 °C above normal, in order to facilitate passive heat loss and minimise EWL thus conserving water at high T_a or when water is scarce (Calder and King 1974; Weathers 1981; Withers and Williams 1990; Tieleman & Williams 1999). However, if birds can no longer evaporate water fast enough to balance heat gain (Tieleman & Williams 1999; McKechnie & Wolf 2010), the increase in T_b may become uncontrollable and T_b could rise to lethal levels (estimated to be between 46° and 47 °C, Dawson & Schmidt-Nielsen 1964). None of the individuals in this study approached these predicted lethal T_b s. This probably reflects the limited experimental T_a range that was achievable (maximum T_a at which data were attained for an individual bird was 41.8 °C in Cape Sugarbird), since birds became increasingly restless at high T_a s and were then removed from the chamber to avoid injury. In addition, birds were removed from the chamber at early signs of distress when T_b was high (~ 43 °C). This was because I was unsure of lethal temperatures in these Fynbos species and because cloacal T_b measurements underestimate deep core temperature (McKechnie & Lovegrove 2003), particularly in birds that are active, in which case these birds may have been closer to lethal T_b than they appeared.

Body temperature data could not be collected for every individual in the study. While the thermocouple used to measure cloacal T_b of the birds was effective in most birds, it was removed by some individuals resulting in a loss of usable T_b data for those birds. Thermocouples are less invasive than surgery; however, implantable temperature-sensitive passive integrated transponder (PIT) tags may be a better option for measuring T_b in future studies.

Dietary guild and endemism to the Fynbos biome

Diet and endemism to the Fynbos biome did not explain any of the variation in physiological patterns observed in this study. For example, while my data seemed to suggest that in general nectarivores had higher T_{ewl} , T_b inflection point and T_{pant} values than granivores and insectivores, the overriding effect of body mass negated these apparent differences since nectarivorous species in my study were generally smaller than species from the other two dietary guilds.

This appears to be a global pattern as nectar-feeding birds are generally relatively small, ranging from 2 g (Bee Hummingbird (*Mellisuga helenae*)) to 150 g (certain honeyeaters e.g. Yellow Wattlebird (*Anthochaera paradoxa*), Gartrell 2000), with the majority of species weighing between 3 and 30 g (Brown et al. 1978). Interestingly, in my study the nectarivorous Malachite Sunbird (mean $M_b = 15.1$ g) had a higher mean T_{ewl} (35.5 °C) and T_{pant} (35.8 °C) than the similar-sized granivorous Cape Canary (mean $M_b = 15.0$ g; mean $T_{\text{ewl}} = 34.9$ °C; mean $T_{\text{pant}} = 34.1$ °C) and insectivorous Victorinø Warbler (mean $M_b = 16.6$ g; mean $T_{\text{ewl}} = 34.7$ °C; mean $T_{\text{pant}} = 33.9$ °C). This seems to suggest that nectarivores may have a higher heat tolerance regardless of their size and requires investigation with a larger sample size. It would also be interesting to compare the physiological response to high T_a of a larger nectarivore (such as one of the honeyeaters (Meliphagidae)) to that of a similar-sized granivorous or insectivorous species to determine whether this is a real trend.

In my study, I did not consider where in the environment a particular species forages (e.g. in trees, on rocks, on the ground). Foraging location may be a more important component of foraging guild than diet, when it comes to predicting the time that different species spend dissipating heat (Louw 2011). Louw (2011) found that arboreal birds spend the least time on evaporative cooling since they forage primarily in the shade of trees canopies (Louw 2011; see also Bartholomew & Cade 1963; Tieleman & Williams 2002b; Kotzen 2003). Given that temperatures are highest directly above the ground (Tieleman & Williams 2002b; Kotzen 2003) and that rocks generally heat up faster than the surrounding ground, Cape Rockjumper which forages primarily on the ground and on rocks (Hockey et al. 2005), may be restricted more and more to the shady sides of gullies in the mountains and might

not be able to continue foraging in the middle of the day as temperatures rise. By contrast, species such as Victorinø Warbler, which generally forages in dense vegetation along watercourses and seeps (Hockey et al. 2005), may be more buffered than other taxa in terms of the trade-off between foraging and thermoregulation at high T_a s. This is a useful avenue for future studies to explore.

Fynbos birds in a global context

The 12 Fynbos bird species that I studied followed a similar body mass-driven pattern of EWL in response to increasing air temperature to that of 33 other species (Appendix C, Table C1). Larger species started increasing EWL at lower T_a s, but showed a more gradual increase in EWL at T_a s above this point.

The magnitude of EWL increase above T_{ewl} was similar for all species, but on average, the Fynbos species had lower inflection points. The fact that, after accounting for body mass, there was no significant difference in the slope of the line above T_{ewl} between Fynbos species and the other species suggests that the EWL response to increasing T_a once the inflection temperature has been reached, is relatively constant and T_{ewl} may thus be a better predictor of a speciesø relative tolerance of high temperatures in terms of EWL.

Based on the regression derived by McKechnie & Wolf (2010) from which the majority of additional data for other species were extracted, the expected T_{ewl} inflection point for a bird of similar mass to Southern Double-collared Sunbird (the smallest species studied) is 38.4 °C, while the expected slope above T_{ewl} is 5.21 mg/g/h/°C. In my study, this species had a slightly higher slope (6.04 mg/g/h/°C) than expected, while the inflection point was lower at 36.0 °C. Expected T_{ewl} for Cape Rockjumper (the largest species studied) is 36.4 °C, while the expected slope above T_{ewl} is 1.98 mg/g/h/°C. The mean slope for Cape Rockjumper was very similar (1.63 mg/g/h/°C) to this expected value, although mean T_{ewl} was much lower (31.2 °C). The fact that T_{ewl} was lower in both species may suggest slight differences in experimental design between my study and others. For example, McKechnie & Wolf (2010) compiled data from studies that tested birds at T_a s starting from 42.5 °C, which is already

higher than the maximum T_a to which the Fynbos birds were exposed. This may explain some of the variation between my study species and the species from other studies.

Alternatively, the generally lower T_{ewl} inflection points in Fynbos birds might be explained by the broadly defined climatic zone in which the majority of the species' distributions are centered (Kottek et al. 2006). Fynbos species comprise the majority of the temperate zone species (i.e. 11 of the 12 species are considered temperate zone species, along with only three other species from the global data set, Appendix C, Table C1). Compared to species from the other three climatic zones, temperate zone birds had the lowest T_{ewl} as a function of M_b , followed by cosmopolitan birds, tropical birds and desert birds, which had the highest T_{ewl} s (Appendix C, Table C3). This makes sense considering that the temperate zone is characterised by the lowest air temperatures of the three broad zones (excluding cosmopolitan) defined for this study (Kottek et al. 2006). Temperate zone species are therefore likely to be most adapted for life at cooler temperatures and may face the greatest challenges from climate warming.

Interestingly, even at a global scale, Cape Rockjumper appears to be an outlier in terms of its low tolerance of high temperatures. For its mass, Cape Rockjumper had a substantially lower mean T_{ewl} compared to similar-sized birds from other regions. For example, the Cape Rockjumper's mean T_{ewl} of 31.2 °C is 9.0 °C lower than the T_{ewl} of a 41.1 g desert-dwelling species, the White-browed Sparrow-weaver (*Plocepasser mahali*), and 3.1 °C lower than the T_{ewl} of a 80.4 g tropical species, the Monk Parakeet (*Myiopsitta monachus*). This hints at the possibility that Cape Rockjumper may have a lower capacity for heat stress or that it may have to start heat dissipating from lower T_a s than other birds of comparable body size, which does not bode well for it given current and future projected climate scenarios (Midgley et al. 2003). It would be interesting to compare the heat tolerance of this species to that of a similar-sized temperate species, since the three temperate species from other studies used here were much smaller than Cape Rockjumper. I also recommend that future studies look into the Cape Rockjumper's acclimation capacity to heat. It is important to know whether the low heat tolerance observed here is a phenotypic response to the cold climate these birds generally

experience or whether they are physiologically fixed with a preference for cooler temperatures; this will be crucial in light of future warming.

While these results provide some valuable insights, the broad climate zone classification used in my study limits their interpretation. This is because, for example, the so-called "tropics" contain a diverse range of habitats ranging from deserts to rain forests (Weathers 1997). Amongst the desert-dwelling species in the global multispecies analysis, Dune Lark (*Certhilauda erythrochlamys*) has the lowest T_{cwl} for its size. However, this species occurs in the Namib Desert, which, due to its proximity to the cool Benguela current in the Atlantic Ocean, rarely experiences $T_a > 40$ °C, unlike most other deserts from which data were extracted (Williams 1999). It is therefore essential to consider local ecological conditions in such large multi-species comparative studies (Weathers 1997). Future studies wishing to compare species' responses to air temperatures at a global scale would benefit from grouping species according to a more quantitative measure such as annual mean temperature of the region in which the majority of the species' distribution is centered, as well as considering differences in species in terms of diet, foraging guild and behaviour (Tieleman et al. 2002).

Phenotypic plasticity in avian thermal tolerance

A fundamental issue that will require thorough investigation in future studies is whether the lower heat tolerance of the Fynbos species, compared to that of other species globally, is a trait that is fixed within their genotypes or whether these birds will be able to adjust their physiological responses as they are faced with progressively hotter conditions under future climate change scenarios. For example, an individual may be able to cope better with increasing air temperatures if it is able to increase its T_{cwl} as T_a increases, thus preventing the need for enhanced thermoregulatory efforts (Piersma & Drent 2003). This so-called "phenotypic plasticity" can manifest itself in numerous ways. For example, developmental plasticity involves irreversible variation in individual traits as a result of environmental variation during ontogeny (Tieleman & Williams 2002a, Piersma & Drent 2003). Another arm of phenotypic plasticity is phenotypic flexibility, which involves reversible changes in traits within in a single adult individual (Tieleman & Williams 2002a, Piersma & Drent 2003).

Currently, most available data on avian phenotypic plasticity describe phenotypic flexibility, while very little is known about developmental plasticity in birds (Piersma and Drent 2003). Furthermore, most studies have investigated how mammals and birds respond to acclimation or acclimatisation to cold environments by increasing heat production (McKechnie 2008, Glanville & Seebacher 2010), whereas considerably less focus has been placed on how phenotypic flexibility influences an endotherm's tolerance for high T_a s.

At high altitudes, reduced oxygen and T_a place strain on avian gas exchange and metabolism (Clemens 1988). Individuals that can adjust thermal physiological traits in response to rapid changes in the environment, should thus incur significant fitness benefits (Piersma and Drent 2003). Birds are capable of enhancing resistance to cold in winter and heat in summer, and have been shown to adjust thermal resistance in response to experimental stimuli (Dawson 2003). For example, many birds have been shown to display phenotypic flexibility in basal metabolic rate (BMR) during acclimatisation to cooler or warmer environments (reviewed by McKechnie & Swanson 2010).

There are still many questions regarding the potential for avian phenotypic plasticity that need answering before accurate predictions of species' responses to climate change can be made (Boyles et al. 2011). Species with different thermal traits are likely to respond differently to climate warming, but to what extent this will occur remains to be seen. In addition, while phenotypic plasticity may diminish the effect of climate change on endotherms, there are physiological limits to how plastic an organism's thermal traits will be, since endothermic thermoregulation is metabolically costly (Boyles et al. 2011). In order for evaporative cooling to occur, the T_b of the organism must be higher than the T_a . Therefore, if endotherms are to adapt to hotter and more humid environments, they would need to increase T_b , which will only be possible up to a certain point given that endothermic T_b s are generally maintained close to lethal limits (Boyles et al. 2011). It is also still unclear how short-term, but increasingly frequent, extreme climatic events, such as heat waves and droughts, will affect endotherms or will organisms have enough time to adapt to these transient weather anomalies and, if so, will individuals with certain traits be favoured (Boyles et al. 2011)? Future research will need to investigate how rapidly and to what extent endotherms are capable of acclimating and acclimatising to

a rapidly changing environment, particularly increasing T_{as} , and how this might affect their fitness. In addition, studies should investigate the contribution of developmental plasticity to phenotypic plasticity in avian species.

Conservation implications

The results of this study have important implications for the conservation of Fynbos bird species in light of future climate warming. Smaller birds may be more susceptible to dehydration at high air temperatures given their higher rates of mass-specific EWL, but will most likely be able to counter extensive water loss by maximising the use of cooler, shaded microsites in their environment. On the other hand, larger species are more likely to suffer from hyperthermia than dehydration as temperatures rise and may have to spend more time thermoregulating than smaller species. Tailored conservation strategies can be implemented in regions with high concentrations of vulnerable species. For example, artificial shaded areas that provide cool microsites or waterholes that provide additional water can be erected in regions with limited natural shade and water in an attempt to overcome some of the difficulties birds may have to face under climate warming (McKeechnie et al. 2012). However, in mountain Fynbos regions where shade and water may be relatively abundant year round, heat-intolerant species will most likely just move to south-facing slopes as it gets hotter to avoid direct sunlight. These slopes therefore should be preserved and protected as far as possible from development and the invasion of alien vegetation. A greater concern may be potential long-term changes in vegetation (for example, an increased risk of extinction of the Proteaceae due to an increase in the frequency of fires in the Fynbos biome (van Wilgen et al. 1992; Brooks et al. 2004)), which may alter habitat structure and the availability of shaded microsites on mountain slopes, forcing birds to alter their use of the landscape. More research on this topic is required in the Fynbos biome.

An important finding from my study is the likely vulnerability of the Cape Rockjumper, which increased EWL at much lower temperatures than the other Fynbos species, as well as similar-sized species globally. Other studies have also tentatively identified this species as being particularly at risk of the effects of climate warming, given its preference for cooler, high altitude regions (Simmons et

al. 2004). In addition, Cape Rockjumper has a severely limited range and recent bioclimatic envelope modelling suggests that it has the most temperature-limited range of all endemic Fynbos bird species (A. T. K. Lee and P. Barnard, unpublished data). Despite this, the species is not recognised by the IUCN as threatened. I recommend that Cape Rockjumper qualifies for a higher IUCN status because, in addition to its low physiological heat tolerance, its habitat is largely fragmented, it is estimated to have a range of less than 20 000 km² (A. T. K. Lee and P. Barnard, unpublished data) and its range is projected to decrease in extent by ~62% by 2085 (Huntley & Barnard 2012).

Researchers and conservationists should start paying more attention to species for which climatic variables are known to be important limiting factors, but which are not currently listed as threatened on the IUCN RedList. In the hands of the rapidly changing human landscape, these species could easily become threatened in the near future (Julliard et al. 2004; Hulme 2005).

Limitations of this study and recommendations for future work

It is important to understand the limitations of the specific methodologies used in this study (and similar studies), in order to interpret results accurately and compare findings with those from other studies. Here, I measured the responses of birds, in terms of EWL, RMR and T_b , to increasing T_a in an open flow-through respirometry chamber. In the wild, birds experience ambient temperatures, which are influenced by wind (Bakken et al. 1981), solar radiation (Lustick et al. 1979; Battley et al. 2003) and forced convection (Wolf 2000). The results in my study reflect only responses to air temperatures and therefore may not be an accurate reflection of the physiological responses of these birds under environmental conditions. My study aims instead to provide a basis for interspecific comparisons. Furthermore, it is essential that physiological data are backed up by behavioural studies, and vice versa, to create a more rounded picture of the thermoregulation of birds.

Since short-term acclimatisation or acclimation to high T_a s has been shown to alter both cutaneous and respiratory EWL in birds (Ophir et al. 2002; McKechnie & Wolf 2004), birds in this study ideally should have been processed at higher temperatures on hotter days and at lower temperatures on cooler

days. This would have proven difficult given that some birds were held overnight or longer before being processed while others were processed directly after capture. However, it remains an important consideration for future studies.

While a moult score was assigned to each bird that was captured, the number of birds that were moulting was not taken into consideration in the analysis. Moulting increases metabolic demands and impairs insulation, which may affect the birds' capacity for thermoregulation (Dietz et al. 1992; Jenni & Winkler 1994). In addition, feather production costs are generally higher in smaller birds due to their higher mass-specific basal metabolic rates (reviewed in Lindstrom et al. 1993). Therefore, moult status may be an important variable to consider in future research on thermal tolerances in birds.

Sex could not be used to influence the choice of study animals at the time of sampling. This was because capturing was often unpredictable and time-consuming so it was not always possible to get a 50:50 ratio among sexually dimorphic species, and non-dimorphic species can only be sexed at a later stage using genetic markers. However, it has been shown that thermoregulatory responses may differ between sexes in birds (Kaiser & Bucher 1985) and bats (Cryan & Wolf 2003), which warrants further investigation in the Fynbos bird species.

My sample sizes (ranging from five to 11 individuals per species) are similar to those of other interspecific studies in birds, which have used sample sizes ranging from, for example, one to 12 individuals per species (Lasiewski & Seymour 1972) or between four and eight individuals per species (Smit & McKechnie 2010). However, these sample sizes are still relatively small and may limit the statistical rigour of my results. Difficulties experienced while capturing birds for this study contributed to the limited sample size. Since the field season coincided with the breeding season of the majority of the species (Hockey et al. 2005), capturing non-breeding birds was difficult. In addition, Protea Seedeater, Victorin's Warbler and Cape Rockjumper are rare and inconspicuous species, making capturing labour-intensive and time-consuming. Further logistical and weather-related issues also reduced capture rates. To improve statistical rigour, any findings from this study should be supported with additional research using more individuals and should ideally contain an

equal sample size for each species. Furthermore, this study should be replicated in different populations occurring in various regions of the Fynbos biome and should be repeated during different seasons, because populations can show highly varied thermoregulatory responses, both spatially and temporally (Smit et al. 2013).

5. Conclusion

The importance of biodiversity for society is often recognised only through its loss (Cherrier et al. 2004). Bird ranges and populations are declining across the globe, which will likely cause substantial alterations in ecosystem processes and overall resilience (Chapin et al. 2000). Disconcertingly, this may only be the tip of iceberg since animals from other taxa are up to 2.5 times more threatened than birds (Cherrier et al. 2004). It is essential that early action is taken to prevent losses in species that are not listed as threatened as well as to prevent further declines in populations of threatened species.

This study confirmed a strong effect of body size on the EWL responses to increasing $T_{a,s}$ in 12 species of birds in the Fynbos biome. Larger species are likely to increase thermoregulatory effort at lower temperatures, but at a more gradual rate compared to smaller species. This is in line with the general trend observed in other birds, suggesting that larger birds may be more prone to hyperthermia while smaller birds are more likely to become dehydrated at high $T_{a,s}$. Although dehydration may be more of a problem for desert-dwelling animals, hyperthermia may be more problematic in the temperate Fynbos biome. In addition, larger birds may have to spend more time in the shade as temperatures rise, since smaller birds can easily move in and out of cooler microsites, dumping heat faster than larger birds and may thus be able to stay active for longer.

The Cape Rockjumper may be deserving of special attention, as it increased EWL at the lowest temperatures for its body size, especially when compared to similar-sized species at a global scale. In addition, it is an altitude-restricted species that will most likely not be able to move further uphill to stay within a favourable cool climatic zone as temperatures warm.

Characterising the mechanisms underlying relative vulnerabilities of different Fynbos bird species to climate warming is important for validating future predictions of species ranges made by bioclimatic envelope models. It furthermore serves as an important step in the development of targeted conservation strategies and provides insight into the possible alterations in the ecological structure and functioning of the Fynbos avian community in the near future.

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Appendix A: Thermal physiological attributes of Blue Hill Nature Reserve species

Table A1. Evaporative water loss (EWL) measures for all 12 BHNr study species, showing the sample size (n) of each species, the outcomes of the Davie's Test for a change in slope, the inflection point in the relationship between air temperature (T_a) and EWL (T_{ewl}, °C) as determined by the segmented model, as well as the outcomes of the linear mixed effects model for the slope (Beta, mg/g/h/°C) of the segment above the T_{ewl}, whether this inflection point was significant or not for the particular species.

Species	n	Davie's Test for change in slope		T _{ewl} (°C, segmented model)		Slope (mg/g/h/°C, linear mixed effects model)						
		p	Significance	Estimate	Std. Error	Intercept	Beta	Std. Error	Df	t	p	Significance
Cape Sugarbird	11	0.000	***	34.6	0.6	-62.82	2.06	0.24	10	8.73	0	****
Orange-breasted Sunbird	10	0.006	**	36.7	1.0	-202.07	5.97	0.87	4	6.89	0.002	**
Cape Siskin	10	0.000	***	35.6	0.5	-156.53	4.72	0.33	7	14.49	0	****
Protea Seed eater	9	0.000	***	33.5	0.6	-91.37	3.03	0.30	12	10.26	0	****
Victorin's Warbler	6	0.091		34.7	1.1	-81.14	2.82	0.57	2	4.96	0.038	*
Cape Rockjumper	10	0.000	***	31.2	0.6	-47.25	1.63	0.13	20	12.83	0	****
Malachite Sunbird	5	0.000	***	35.5	0.6	-170.95	5.34	0.30	4	17.56	0.000	***
Southern Double-collared Sunbird	10	0.000	***	36.0	0.5	-199.87	6.04	1.14	4	5.31	0.006	*
Cape Canary	4	0.000	***	34.9	0.6	-132.58	4.27	2.41	0	1.77	NA	NA
Cape Bunting	10	0.000	***	35.3	0.4	-117.21	3.65	0.40	7	9.17	0.000	***
Cape Grassbird	5	0.164		33.4	1.4	-71.75	2.36	0.21	7	11.36	0	****
Familiar Chat	10	0.000	***	33.5	0.5	-90.28	2.89	0.37	9	7.89	0.000	***

* p < 0.05

** p < 0.01

*** p < 0.001

**** p = 0

NA ó too few data points

Table A2. Resting metabolic rate (RMR) measures for all 12 study species, showing the sample size (n) of each species, the outcomes of the Davieø Test for a change in slope, the inflection point (°C) in the relationship between air temperature (T_a) and RMR as determined by the segmented model, as well as the outcomes of the linear mixed effects model for the slope (Beta, J/g/h/°C) of the segment above significant inflection points or, in the case of Familiar Chat, for the segment below the inflection point. In cases where the Davieø Test showed no significant change in slope and therefore no significant RMR inflection point, the slope was calculated for the entire dataset and not only for the segment above (or below) the point, and these values are shown here. Where it was suspected that the inflection point was indicative of a lower limit of thermoneutrality as opposed to an upper limit, the Davieø Test was conducted on data above this point; but in all such cases the outcomes were non-significant.

Species	N	Davie's Test for change in slope		RMR inflection point (°C, segmented model)		Slope (J/g/h/°C, linear mixed effects model)						
		p	Significance	Estimate	Std. Error	Intercept	Beta	Std. Error	Df	T	p	Significance
Cape Sugarbird	11	0.011	*	26.7	0.6	58.80	-0.73	0.23	29	-3.16	0.004	**
Orange-breasted Sunbird	10	0.474				172.20	-3.28	0.64	29	-5.16	0	****
Cape Siskin	10	0.046	*	27.3	1.1	47.25	0.13	0.54	28	0.23	0.819	
Protea Seedeater	6	0.377		38.0	0.2	86.15	-0.54	0.29	20	-1.85	0.079	
Victorin's Warbler	6	0.622		27.2	0.3	132.51	-2.02	0.54	17	-3.77	0.002	**
Cape Rockjumper	7	0.164		22.4	0.1	44.42	-0.28	0.16	22	-1.78	0.089	
Malachite Sunbird	3	0.090		33.0	1.6	13.25	0.67	0.36	10	1.87	0.091	
Southern Double-collared Sunbird	10	0.037	*	31.2	1.6	-24.33	2.81	1.47	12	1.91	0.080	
Cape Canary	3	0.024	*	30.8	1.1	48.06	0.15	1.34	3	0.11	0.921	
Cape Bunting	6	0.444		35.4	2.0	68.56	-0.70	0.32	19	-2.19	0.041	*
Cape Grassbird	3	0.344		36.1	59.8	177.69	-3.23	0.51	12	-6.33	0	****
Familiar Chat	6	0.000	****	30.3	1.6	174.84 ^a	-3.86 ^a	0.91 ^a	3 ^a	-4.27 ^a	0.024 ^a	* ^a

^a Values are for the segment below the inflection point

* p < 0.05

** p < 0.01

*** p < 0.001

**** p = 0

NA ó too few data points

Table A3. Body temperature (T_b) measures for all 12 study species, showing the sample size (n) of each species, the outcomes of the Davieø Test for a change in slope, the inflection point ($^{\circ}\text{C}$) in the relationship between air temperature (T_a) and T_b as determined by the segmented model, as well as the outcomes of the linear mixed effects model for the slope (Beta, $\text{mg/g/h}^{\circ}\text{C}$) of the segment above significant inflection points. In cases where the Davieø Test showed no significant change in slope and therefore no significant T_b inflection point, the slope was calculated for the entire dataset and not only for the segment above the point, and these values are shown here.

Species	n	Davie's Test for change in slope		T_b inflection point ($^{\circ}\text{C}$, segmented model)		Slope ($^{\circ}\text{C } T_b / ^{\circ}\text{C } T_a$, linear mixed effects model)						
		p	Significance	Estimate	Std. Error	Intercept	Beta	Std. Error	Df	T	p	Significance
Cape Sugarbird	11	0.000	***	30.7	1.0	27.77	0.36	0.03	21	13.00	0	****
Orange-breasted Sunbird	8	0.000	***	34.7	0.4	21.97	0.52	0.03	9	15.45	0	****
Cape Siskin	9	0.066		34.3	1.3	35.39	0.17	0.02	28	7.07	0	****
Protea Seed eater	7	0.000	***	30.9	0.9	30.88	0.27	0.05	14	5.80	0	****
Victorin's Warbler	5	0.187		27.5	0.2	35.35	0.16	0.04	14	4.30	0.001	***
Cape Rockjumper	4	0.000	***	32.1	0.8	26.90	0.38	0.03	5	14.97	0	****
Malachite Sunbird	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Southern Double-collared Sunbird	8	0.000	***	35.2	0.6	15.44	0.68	0.09	5	7.50	0.001	***
Cape Canary	3	0.929		31.8	2.7	39.34	0.02	0.04	9	0.63	0.547	
Cape Bunting	10	0.000	***	32.6	0.8	25.72	0.42	0.02	13	20.03	0	****
Cape Grassbird	2	0.047	*	30.8	0.9	31.91	0.25	0.04	4	5.66	0.005	**
Familiar Chat	8	0.000	***	33.3	0.7	26.41	0.41	0.05	5	8.26	0.000	***

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

**** $p = 0$

NA ó too few data points

Table A4. Mass-specific evaporative water loss (EWL, mg/g/h), resting metabolic rate (RMR, J/g/h) and body temperature (T_b , °C) at air temperature of 30° and 38 °C for each of the 12 species at Blue Hill Nature Reserve, showing standard error (Std. Error) for each measure, the number of individuals included in the calculation of these values (n (30), n (38)) as well as the change in the abovementioned values between 30° and 38 °C (Change (30-38)) calculated by dividing the value at 38 °C by that at 30 °C.

	EWL (mg/g/h)							RMR (J/g/h)							T_b (°C)						
	30°C	Std. Error	n (30)	38°C	Std. Error	n (38)	Change (30-38)	30°C	Std. Error	n (30)	38°C	Std. Error	n (38)	Change (30-38)	30°C	Std. Error	n (30)	38°C	Std. Error	n (38)	Change (30-38)
CSB	7.16	0.74	5	16.37	0.75	6	2.29	36.54	6.78	5	34.81	3.49	6	0.95	39.4	0.3	5	41.0	0.3	6	1.0
OBS	12.98	1.41	5	24.58	4.41	6	1.89	66.00	8.31	5	56.79	11.72	6	0.86	40.3	0.4	3	41.6	0.2	5	1.0
CS	9.23	2.23	3	21.22	2.31	5	2.30	36.89	9.23	3	60.60	10.69	5	1.64	40.2	0.4	3	42.4	0.4	4	1.1
PS	7.95	1.03	5	26.65	1.30	5	3.35	69.65	10.37	4	75.39	5.93	3	1.08	39.3	0.2	5	41.3	0.3	3	1.1
VW	11.12	1.43	3	28.28	NA	1	2.54	44.80	5.56	3	81.10	NA	1	1.81	39.7	0.0	2	41.3	NA	1	1.0
CRJ	3.42	0.27	5	15.10	1.14	5	4.41	37.05	1.28	4	32.15	3.35	3	0.87	39.3	0.2	3	41.4	NA	1	1.1
MSB	11.76	1.54	2	34.29	1.92	3	2.92	31.79	4.05	2	41.75	NA	1	1.31	38.2	NA	1	NA	NA	NA	NA
SDCS	14.17	1.90	5	28.97	2.29	5	2.04	52.02	10.78	3	96.53	10.01	5	1.86	39.4	0.1	3	41.5	0.2	5	1.1
CC	12.16	2.33	3	33.92	NA	1	2.79	55.45	2.54	1	NA	NA	NA	NA	39.9	0.2	3	NA	NA	NA	NA
CB	7.94	0.63	7	21.99	1.68	5	2.77	42.96	6.83	5	58.47	9.02	2	1.36	39.4	0.2	7	41.7	0.3	5	1.1
CG	9.75	2.47	6	18.53	1.23	3	1.90	79.23	1.74	3	60.69	6.78	2	0.77	39.6	0.2	2	41.2	NA	1	1.0
FC	6.69	0.48	6	20.73	2.00	5	3.10	59.34	3.43	3	67.21	4.04	4	1.13	40.0	0.2	6	42.1	0.2	2	1.1

Appendix B: Interspecific comparison of Blue Hill Nature Reserve species

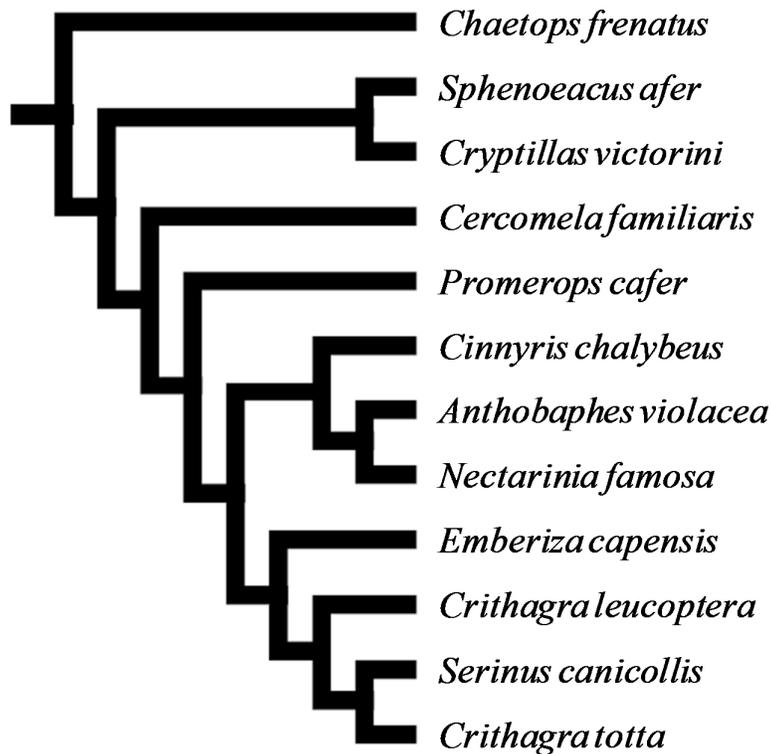


Figure B1. Phylogeny of the 12 bird species in which various physiological parameters were investigated at Blue Hill Nature Reserve, Western Cape, South Africa. This phylogenetic tree represents the majority consensus tree from 100 hypothetical phylogenies that were sampled for each data set from <http://www.birdtree.org> (Jetz et al. 2012) using the Hackett et al. (2008) phylogeny as backbone.

Table B2. Area under the receiver operating characteristics curve (AUC) scores for two climatic variables, namely annual mean temperature (ME1) and maximum temperature of the warmest month (ME2), from MaxEnt model data (A.T.K. Lee and P. Barnard, unpublished data) for each of the 12 species studied at Blue Hill Nature Reserve, Western Cape, South Africa.

Species	AUC score for annual mean temperature (ME1)	AUC score for maximum temperature of warmest month (ME2)
Cape Sugarbird	0.59	0.55
Orange-breasted Sunbird	0.60	0.59
Cape Siskin	0.65	0.54
Protea Seedeater	0.66	0.51
Victorin's Warbler	0.54	0.61
Cape Rockjumper	0.85	0.79
Malachite Sunbird	0.55	0.56
Southern Double-collared Sunbird	0.59	0.55
Cape Canary	0.53	0.55
Cape Bunting	0.62	0.60
Cape Grassbird	0.55	0.60
Familiar Chat	0.66	0.57

Table B3. A summary of the three best-fitting conventional and phylogenetic independent contrast (PIC) models used to compare four measures of evaporative water loss (EWL), three measures of body temperature (T_b), and the mean onset of panting temperature (T_{pant}) between all 12 study species in terms of the species' log body mass (Log M_b), dietary guild (Diet) and endemism to the Fynbos biome (Endemism) as well as the degree to which its distribution is limited by annual mean temperature (ME1) and maximum temperature of the warmest month (ME2), according to A.T.K. Lee and P. Barnard (unpublished data). In each case, AIC_c (Akaike's Information Criterion with correction for small sample sizes) values were compared to select the best-fitting model from a selection of seven different models for each of the above parameters (Figure B1). In cases where AIC_c values were very similar ($\hat{\epsilon} AIC_c < 2$), the simplest nested model with the least explanatory factors was selected as the best model, following Arnold (2010). Shown here are the three best-fitting models for each parameter with their respective AIC_c and $\hat{\epsilon} AIC_c$ (with respect to the best-fitting model) values. The best model is presented in bold.

Physiological parameter	Analysis	Three best-fitting models	AIC_c	ΔAIC_c
T_{ewl}	Conventional	$T_{\text{ewl}} \sim \text{Log } M_b$	36.08	0.00
		$T_{\text{ewl}} \sim \text{Log } M_b + \text{ME1}$	37.30	1.22
		$T_{\text{ewl}} \sim \text{Log } M_b + \text{ME2}$	39.76	3.68
	PIC	$T_{\text{ewl}} \sim \text{Log } M_b$	-1.80	0.00
		$T_{\text{ewl}} \sim \text{Log } M_b + \text{ME1}$	2.09	3.89
		$T_{\text{ewl}} \sim \text{Log } M_b + \text{ME2}$	3.01	4.81
Log EWL Slope	Conventional	Log EWL Slope $\sim \text{Log } M_b$	-25.89	0.00
		Log EWL Slope $\sim \text{Log } M_b + \text{Endemism}$	-22.42	3.47
		Log EWL Slope $\sim \text{Log } M_b + \text{ME1}$	-21.18	4.71
	PIC	Log EWL Slope $\sim \text{Log } M_b$	-59.03	0.00
		Log EWL Slope $\sim \text{Log } M_b + \text{ME1}$	-54.96	4.07
		Log EWL Slope $\sim \text{Log } M_b + \text{ME2}$	-54.91	4.12
EWL at 30 °C	Conventional	EWL 30 $\sim \text{Log } M_b * \text{ME1}$	42.63	0.00
		EWL 30 $\sim \text{Log } M_b + \text{ME1}$	47.23	4.60
		EWL 30 $\sim \text{Log } M_b$	52.84	10.21
	PIC	EWL 30 $\sim \text{Log } M_b * \text{ME1}$	5.00	0.00
		EWL 30 $\sim \text{Log } M_b + \text{ME1}$	5.52	0.52
		EWL 30 $\sim \text{ME1}$	16.93	11.93
EWL change from 30° - 38 °C	Conventional	EWL change $\sim \text{ME1}$	24.02	0.00
		EWL change $\sim \text{Log } M_b + \text{ME1}$	27.31	3.29
		EWL change $\sim \text{Log } M_b$	29.26	5.24
	PIC	EWL change $\sim \text{Log } M_b$	-8.63	0.00
		EWL change $\sim \text{ME1}$	-4.66	3.97
		EWL change $\sim \text{Log } M_b + \text{ME1}$	-4.28	4.34

T _b inflection point	Conventional	T _b IP ~ Log M _b + ME1	53.65	0.00
		T_b IP ~ Log M_b	53.85	0.20
		T _b IP ~ ME1	56.50	2.85
	PIC	T_b IP ~ ME1	18.91	0.00
		T _b IP ~ Endemism	20.30	1.39
		T _b IP ~ Log Mb	20.33	1.42
T _b at 30 °C	Conventional	T _b 30 ~ Endemism	26.97	0.00
		T_b 30 ~ Log M_b	27.31	0.34
		T _b 30 ~ ME1	27.86	0.89
	PIC	T_b 30 ~ Log M_b	-5.60	0.00
		T _b 30 ~ Log M _b *Endemism	-4.93	0.66
		T _b 30 ~ Endemism	-4.28	1.31
T _b change from 30° - 38 °C	Conventional	T_b change ~ ME1	13.33	0.00
		T _b change ~ Endemism	14.05	0.72
		T _b change ~ ME2	15.23	1.90
	PIC	T_b change ~ ME1	-14.34	0.00
		T _b change ~ Log M _b	-13.85	0.48
		T _b change ~ Endemism	-13.63	0.71
T _{pant}	Conventional	T_{pant} ~ Log M_b	44.08	0.00
		T _{pant} ~ Log M _b + Diet	47.04	2.96
		T _{pant} ~ Log M _b + ME1	47.80	3.72
	PIC	T_{pant} ~ Log M_b	4.60	0.00
		T _{pant} ~ Log M _b + ME1	7.02	2.42
		T _{pant} ~ Log M _b + Endemism	8.32	3.72

Table B4. A summary of the outcomes of the best conventional and phylogenetic independent contrast (PIC) model for each physiological parameter compared between the 12 study species. In cases where a single best model could not be selected, results are shown for the two or three best (i.e. simplest nested) models. EWL = evaporative water loss, T_b = body temperature, T_{pant} = air temperature at which panting began, M_b = body mass, ME1 = MaxEnt output for predicting the correlation between species distribution and annual mean temperature.

Physiological parameter	Analysis	Model	Coefficients	Estimate	Std. Error	t	P	Significance
T_{ewl}	Conventional	$T_{\text{ewl}} \sim \text{Log } M_b$	Intercept	41.25	1.33	31.11	0.000	***
			Log M_b	-5.26	1.03	-5.11	0.000	***
	PIC	$T_{\text{ewl}} \sim \text{Log } M_b$	Intercept	-0.05	0.05	-0.91	0.386	
			Log M_b	-4.86	1.32	-3.69	0.005	**
Log EWL Slope	Conventional	Log EWL Slope $\sim \text{Log } M_b$	Intercept	1.47	0.10	14.70	0.000	***
			Log M_b	-0.74	0.08	-9.51	0.000	***
	PIC	Log EWL Slope $\sim \text{Log } M_b$	Intercept	-0.01	0.00	-1.67	0.129	
			Log M_b	-0.61	0.10	-6.27	0.000	***
EWL at 30 °C	Conventional	EWL 30 $\sim \text{Log } M_b^* \text{ ME1}$	Intercept	70.51	12.04	5.86	0.000	***
			Log M_b	-34.88	7.87	-4.43	0.002	**
			ME1	-81.88	19.46	-4.21	0.003	**
			Log $M_b^* \text{ ME1}$	42.66	12.40	3.44	0.009	**
	PIC	EWL 30 $\sim \text{Log } M_b + \text{ ME1}$	Intercept	0.09	0.06	1.43	0.189	
			Log M_b	-8.47	1.59	-5.32	0.001	***
		ME1	-20.73	3.54	-5.85	0.000	***	
EWL change from 30° - 38 °C	Conventional	EWL change $\sim \text{ME1}$	Intercept	-1.11	1.06	-1.04	0.323	
			ME1	6.14	1.70	3.61	0.005	**
	PIC	EWL change $\sim \text{Log } M_b$	Intercept	-0.02	0.04	-0.60	0.562	
			Log M_b	2.37	0.97	2.46	0.036	*
T_b inflection point	Conventional	$T_b \text{ IP} \sim \text{Log } M_b$	Intercept	37.82	3.31	11.44	0.000	***
			Log M_b	-4.43	2.55	-1.74	0.116	*
	PIC	$T_b \text{ IP} \sim \text{ME1}$	Intercept	-0.01	0.16	-0.03	0.973	
			ME1	-5.40	3.97	-1.36	0.211	
	$T_b \text{ IP} \sim \text{Log } M_b$	Intercept	-0.14	0.14	-0.99	0.354		
Log M_b		6.19	8.40	0.74	0.482			

T _b at 30 °C	Conventional	T _b 30 ~ Log M _b	Intercept	40.18	0.92	43.69	0.000	***
			Log M _b	-0.50	0.71	-0.70	0.499	
		T _b 30 ~ ME1	Intercept	39.36	1.25	31.59	0.000	***
			ME1	0.30	2.00	0.15	0.882	
	PIC	T _b 30 ~ Log M _b	Intercept	0.04	0.04	0.82	0.431	
			Log M _b	-2.02	1.11	-1.82	0.102	
T _b change from 30° - 38 °C	Conventional	T _b change ~ ME1	Intercept	0.91	0.77	1.17	0.275	
			ME1	1.57	1.21	1.30	0.230	
		T _b change ~ ME2	Intercept	1.95	0.91	2.15	0.064	
		ME2	-0.08	1.52	-0.05	0.96		
	PIC	T _b change ~ ME1	Intercept	0.00	0.02	-0.10	0.927	
			ME1	1.36	1.80	0.76	0.473	
		T _b change ~ Log M _b	Intercept	0.01	0.03	0.22	0.833	
		Log M _b	-0.27	0.65	-0.42	0.686		
T _{pant}	Conventional	T _{pant} ~ Log M _b	Intercept	40.51	1.85	21.90	0.000	***
			Log M _b	-4.19	1.44	-2.92	0.015	*
	PIC	T _{pant} ~ Log M _b	Intercept	0.04	0.07	0.63	0.547	
			Log M _b	-5.40	1.76	-3.07	0.013	*

* p < 0.05

** p < 0.01

*** p < 0.001

Appendix C: Global multispecies comparison

Table C1. A summary of the physiological data from 45 species used in the global multispecies comparative analysis. This includes data from the 12 species studied at Blue Hill Nature Reserve (BHNR) for this study, data from six species studied by Whitfield, Smit, McKechnie and Wolf (unpublished data) and data extracted from 27 species in the analyses of McKechnie and Wolf (2010). The table includes common and scientific names of species, the broad climatic zone in which the majority of the species' distribution is centered (classified according to W. Köppen in 1900 (updated version: Kottek et al. 2006)), whether the species was studied at BHNR or not (other), mean body mass (M_b , g), the mean inflection point in the relationship between evaporative water loss (EWL) and air temperature (T_{ewl} , °C), the mean slope of the line above this inflection point (EWL slope, mg/g/h/°C) and the source of these data for each species. Cosmo = cosmopolitan.

Common name	Scientific name	Climatic zone	Study	M_b (g)	Log M_b	T_{ewl} (°C)	EWL slope (mg/g/h/°C)	Log EWL slope	Source
Cape Bunting	<i>Emberiza capensis</i>	Temperate	BHNR	19.8	1.3	35.3	3.65	0.56	This study
Cape Canary	<i>Serinus canicollis</i>	Temperate	BHNR	14.9	1.2	34.9	4.27	0.63	This study
Cape Grassbird	<i>Sphenoeacus afer</i>	Temperate	BHNR	30.0	1.5	33.4	2.36	0.37	This study
Cape Rockjumper	<i>Chaetops frenatus</i>	Temperate	BHNR	53.7	1.7	31.2	1.63	0.21	This study
Cape Siskin	<i>Serinus totta</i>	Temperate	BHNR	12.6	1.1	35.6	4.72	0.67	This study
Cape Sugarbird	<i>Promerops cafer</i>	Temperate	BHNR	36.2	1.6	34.6	2.06	0.31	This study
Malachite Sunbird	<i>Nectarinia famosa</i>	Temperate	BHNR	15.2	1.2	35.5	5.34	0.73	This study
Orange-breasted Sunbird	<i>Anthobaphes violacea</i>	Temperate	BHNR	9.4	1.0	36.7	5.97	0.78	This study
Protea Seedeater	<i>Crithagra leucoptera</i>	Temperate	BHNR	19.8	1.3	33.5	3.03	0.48	This study
Southern Double-collared Sunbird	<i>Nectarinia chalybea</i>	Temperate	BHNR	7.5	0.9	36.0	6.04	0.78	This study
Victorin's Warbler	<i>Bradypterus victorini</i>	Temperate	BHNR	17.1	1.2	34.7	2.82	0.45	This study
Chukar Partridge	<i>Alectoris chukar</i>	Temperate	Other	250.0	2.4	32.5	0.58	-0.24	McKechnie & Wolf 2010
Bridled Titmouse	<i>Baeolophus wollweberi</i>	Temperate	Other	10.5	1.0	37.9	5.07	0.71	McKechnie & Wolf 2010
Juniper Titmouse	<i>Baeolophus ridgwayi</i>	Temperate	Other	17.0	1.2	36.3	2.91	0.46	McKechnie & Wolf 2010
Black-rumped Waxbill	<i>Estrilda troglodytes</i>	Tropical	Other	6.0	0.8	38.7	6.28	0.80	McKechnie & Wolf 2010
Double-banded Sandgrouse	<i>Pterocles bicinctus</i>	Tropical	Other	196.7	2.3	34.5	0.70	-0.15	McKechnie & Wolf 2010
Dusky Munia	<i>Lonchura fuscans</i>	Tropical	Other	9.5	1.0	34.7	2.79	0.45	McKechnie & Wolf 2010
Gouldian Finch	<i>Erythrura gouldiae</i>	Tropical	Other	17.1	1.2	36.4	3.18	0.50	McKechnie & Wolf 2010
Marbled Frogmouth	<i>Podargus ocellatus</i>	Tropical	Other	145.0	2.2	37.8	1.61	0.21	McKechnie & Wolf 2010
Monk Parakeet	<i>Myiopsitta monachus</i>	Tropical	Other	80.4	1.9	34.3	1.83	0.26	McKechnie & Wolf 2010
Variable Seedeater	<i>Sporophila corvina</i>	Tropical	Other	10.9	1.0	37.9	4.48	0.65	McKechnie & Wolf 2010
Cape Turtle Dove	<i>Streptopelia capicola</i>	Desert	Other	138.2	2.1	43.3	1.62	0.21	Whitfield et al. 2010
Laughing Dove	<i>Stigmatopelia senegalensis</i>	Desert	Other	86.5	1.9	39.9	1.87	0.27	Whitfield et al. 2010

Namaqua Dove	<i>Oena capensis</i>	Desert	Other	35.8	1.6	40.8	2.50	0.40	Whitfield et al. 2010
Scaly-feathered Weaver	<i>Sporopipes squamifrons</i>	Desert	Other	10.6	1.0	39.3	3.67	0.56	Whitfield et al. 2010
Sociable Weaver	<i>Philetairus socius</i>	Desert	Other	24.9	1.4	42.8	3.17	0.50	Whitfield et al. 2010
White-browed Sparrow-weaver	<i>Plocepasser mahali</i>	Desert	Other	41.1	1.6	40.2	4.01	0.60	Whitfield et al. 2010
Black-bellied Sandgrouse	<i>Pterocles orientalis</i>	Desert	Other	386.4	2.6	31.3	0.28	-0.55	McKechnie & Wolf 2010
MacQueen's Bustard	<i>Chlamydotis undulate</i>	Desert	Other	1248.0	3.1	34.7	0.39	-0.41	McKechnie & Wolf 2010
Budgerigar	<i>Melopsittacus undulates</i>	Desert	Other	33.7	1.5	37.9	3.46	0.54	McKechnie & Wolf 2010
Diamond Dove	<i>Geopelia cuneata</i>	Desert	Other	38.0	1.6	39.4	2.44	0.39	McKechnie & Wolf 2010
Dune Lark	<i>Certhilauda erythrochlamys</i>	Desert	Other	27.3	1.4	36.5	5.34	0.73	McKechnie & Wolf 2010
Dunn's Lark	<i>Eremalauda dunni</i>	Desert	Other	20.6	1.3	39.8	4.54	0.66	McKechnie & Wolf 2010
Greater Hoopoe-lark	<i>Alaemon alaudipes</i>	Desert	Other	37.7	1.6	38.6	4.32	0.64	McKechnie & Wolf 2010
Spinifex Pigeon	<i>Geophaps plumifera</i>	Desert	Other	89.0	1.9	37.7	1.49	0.17	McKechnie & Wolf 2010
Spinifexbird	<i>Eremiornis carteri</i>	Desert	Other	12.0	1.1	37.3	4.10	0.61	McKechnie & Wolf 2010
Spotted Nightjar	<i>Eurostopodus argus</i>	Desert	Other	88.0	1.9	41.1	1.86	0.27	McKechnie & Wolf 2010
Verdin	<i>Auriparus flaviceps</i>	Desert	Other	7.0	0.8	37.8	5.33	0.73	McKechnie & Wolf 2010
White-winged Dove	<i>Zenaida asiatica</i>	Desert	Other	142.2	2.2	NA	1.47	0.17	McKechnie & Wolf 2010
Familiar Chat	<i>Cercomela familiaris</i>	Cosmo	BHNR	20.3	1.3	33.5	2.89	0.46	This study
Burrowing Owl	<i>Athene cunicularia</i>	Cosmo	Other	100.0	2.0	35.6	1.39	0.14	McKechnie & Wolf 2010
Common Nighthawk	<i>Chordeiles minor</i>	Cosmo	Other	72.0	1.9	35.8	1.50	0.18	McKechnie & Wolf 2010
Emu	<i>Dromaius novaehollandiae</i>	Cosmo	Other	40700.0	4.6	29.4	0.14	-0.86	McKechnie & Wolf 2010
Mourning Dove	<i>Zenaida macroura</i>	Cosmo	Other	120.0	2.1	NA	1.30	0.12	McKechnie & Wolf 2010
Pin-tailed Sandgrouse	<i>Pterocles alchata</i>	Cosmo	Other	242.9	2.4	33.0	0.50	-0.30	McKechnie & Wolf 2010

NA ó no Towl estimate in source

Table C2. A summary of all conventional and phylogenetic generalised least squares (PGLS) models used to compare two measures of evaporative water loss (EWL), namely the inflection point in the relationship between air temperature (T_a) and EWL (T_{ewl} , °C) and the slope of the line above this point (Log EWL slope) between 45 species from across the globe (Table C1). Data for these parameters were compared between the 12 species studied during this study at Blue Hill Nature Reserve and 33 species from other published and unpublished data sets (Study, refer to Table C1). All 45 species were also compared in terms of the broad climatic zone in which the majority of their distribution is centered (Climate zone, Kottek et al. 2006). In each case, AIC_c (Akaike's Information Criterion with correction for small sample sizes) values were compared to select the best-fitting model. In cases where AIC_c values were very similar ($\hat{\epsilon} AIC_c < 2$), the simplest model with the least explanatory factors was selected as the best model, following Arnold (2010). Shown in this table are each conventional and PGLS model for each physiological parameter with their respective AIC_c and $\hat{\epsilon} AIC_c$ (with respect to the best-fitting model) values. The model selected as the best model is presented in bold.

Test factor	Analysis	Physiological parameter	Model	AIC_c	ΔAIC_c
Study	Conventional	T_{ewl}	$T_{ewl} \sim \text{Log } M_b + \text{study}$	202.2	0.00
			$T_{ewl} \sim \text{Log } M_b * \text{study}$	203.79	1.59
			$T_{ewl} \sim \text{Log } M_b$	217.34	15.14
		Log EWL Slope	Log EWL Slope $\sim \text{Log } M_b$	-45.30	0.00
			Log EWL Slope $\sim \text{Log } M_b + \text{study}$	-42.90	2.40
			Log EWL Slope $\sim \text{Log } M_b * \text{study}$	-42.47	2.83
	PGLS	T_{ewl}	$T_{ewl} \sim \text{Log } M_b + \text{study}$	191.16	0.00
			$T_{ewl} \sim \text{Log } M_b * \text{study}$	192.42	1.26
			$T_{ewl} \sim \text{study}$	198.58	7.42
		Log EWL Slope	Log EWL Slope $\sim \text{Log } M_b$	-56.20	0.00
			Log EWL Slope $\sim \text{Log } M_b + \text{study}$	-54.53	1.67
			Log EWL Slope $\sim \text{Log } M_b * \text{study}$	-53.84	2.36
Climate zone	Conventional	T_{ewl}	$T_{ewl} \sim \text{Log } M_b + \text{Climate zone}$	195.62	0.00
			$T_{ewl} \sim \text{Log } M_b * \text{Climate zone}$	203.79	8.17
			$T_{ewl} \sim \text{Climate zone}$	206.48	10.86
		Log EWL Slope	Log EWL Slope $\sim \text{Log } M_b$	-45.30	0.00
			Log EWL Slope $\sim \text{Log } M_b * \text{Climate zone}$	-43.23	2.07
			Log EWL Slope $\sim \text{Log } M_b + \text{Climate zone}$	-40.25	5.05
	PGLS	T_{ewl}	$T_{ewl} \sim \text{Log } M_b + \text{Climate zone}$	193.34	0.00
			$T_{ewl} \sim \text{Log } M_b$	199.52	6.18
		Log EWL Slope	$T_{ewl} \sim \text{Log } M_b * \text{Climate zone}$	199.82	6.48
			Log EWL Slope $\sim \text{Log } M_b$	-56.21	0.00
		Log EWL Slope $\sim \text{Log } M_b + \text{Climate zone}$	-55.24	0.98	
		Log EWL Slope $\sim \text{Log } M_b * \text{Climate zone}$	-51.64	4.57	

Table C3. A summary of the outcomes of the best-fitting conventional and phylogenetic generalised least squares (PGLS) model for each of two measures of evaporative water loss (EWL), namely the inflection point in the relationship between air temperature and EWL (T_{ewl}) and the slope of line above this point (Log EWL slope), compared between 45 species in terms of the study used (BHNR or other) and their climate zone (Kottek et al. 2006, Tables C1, C2).

Test factor	Analysis	Model	Coefficients	Estimate	Std. Error	t	P	Significance	
Study	Conventional	$T_{ewl} \sim \text{Log } M_b + \text{study}$	Intercept (BHNR birds)	37.72	0.98	38.64	0.000	***	
			Beta $\text{Log } M_b$	-2.48	0.55	-4.51	0.000	***	
			Intercept (Other birds)	3.82	0.85	4.50	0.000	***	
			Log EWL Slope $\sim \text{Log } M_b$	Intercept	1.17	0.05	21.78	0.000	***
			Beta ($\text{Log } M_b$)	-0.50	0.03	-16.50	0.000	***	
	PGLS	$T_{ewl} \sim \text{Log } M_b + \text{study}$	Intercept (BHNR birds)	37.27	3.15	11.83	0.000	***	
			Beta ($\text{Log } M_b$)	-2.50	0.77	-3.23	0.002	**	
			Intercept contrast (Other birds)	3.27	1.00	3.25	0.002	**	
			Log EWL Slope $\sim \text{Log } M_b$	Intercept	1.01	0.17	5.96	0.000	***
			Beta ($\text{Log } M_b$)	-0.43	0.04	-9.60	0.000	***	
Climate zone	Conventional	$T_{ewl} \sim \text{Log } M_b + \text{Climate zone}$	Intercept (Cosmopolitan birds)	38.38	1.61	23.87	0.000	***	
			Beta ($\text{Log } M_b$)	-2.00	0.53	-3.76	0.001	***	
			Intercept contrast (Desert birds)	3.66	1.15	3.18	0.003	**	
			Intercept contrast (Temperate birds)	-0.86	1.25	-0.68	0.499		
			Intercept contrast (Tropical birds)	0.87	1.34	0.65	0.519		
	PGLS	$T_{ewl} \sim \text{Log } M_b + \text{Climate zone}$	Intercept (Cosmopolitan birds)	40.23	2.99	13.47	0.000	***	
			Beta ($\text{Log } M_b$)	-2.49	0.76	-3.26	0.002	**	
			Intercept contrast (Desert birds)	2.65	1.05	2.52	0.016	*	
			Intercept contrast (Temperate birds)	-0.69	1.13	-0.61	0.545		
			Intercept contrast (Tropical birds)	1.10	1.17	0.94	0.352		
PGLS	Log EWL Slope $\sim \text{Log } M_b$	Intercept	1.01	0.17	5.96	0.000	***		
		Beta ($\text{Log } M_b$)	-0.43	0.04	-9.60	0.000	***		

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$